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Revised Classification of the Species within the *Dryopteris varia* Complex (Dryopteridaceae) in Japan

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The *Dryopteris varia* complex (subg. *Erythrovariae* sect. *Variae* Fraser-Jenk.) is an apogamous fern complex. Most species of the complex are triploid apogamous, show morphological and genetic variation, and present difficulties in their identification. Recent molecular research suggested that the reason that each apogamous species in the complex is so variable is due to reticulate evolution through hybridization between diploid sexual and triploid apogamous species. In this study, we summarized the taxonomic treatment of 11 species within the *D. varia* complex (*D. bissetiana*, *D. chichisimensis*, *D. erythrovaria* sp. nov., *D. hikonensis*, *D. insularis*, *D. kobayashii*, *D. protobissetiana*, *D. sacrosancta*, *D. saxifraga*, *D. subhikonensis* sp. nov., and *D. varia*) on the basis of their genome constituents revealed by molecular analyses.

Key words: apogamous, classification, Dryopteridaceae, hybrid origin, reticulate evolution, the *Dryopteris varia* complex

Dryopteris Adans. (Dryopteridaceae), with 225—c. 400 species recognized (Fraser-Jenkins 1986, Pteridophyte Phylogeny Group 2016), is one of the world's largest genera of ferns. In Japan, 62 species, four varieties and two formae were listed by Iwatsuki (1995). About half of the Japanese species of *Dryopteris* were reported to be apogamous and mostly triploid, rarely diploid or tetraploid (Takamiya 1996).

Apogamous species of *Dryopteris* in Japan often show large and continuous morphological variation, and their identification is difficult. Individuals with intermediate morphology between several species often occur. Such morphological variation has confused Japanese taxonomists, resulting in several apogamous complexes being recognized (Iwatsuki 1995, Lin *et al*. 1995, 2003).

The *Dryopteris varia* complex [subg. *Erythrovariae* (H. Itô) Fraser-Jenk. sect. *Variae* Fraser-Jenk. Lin *et al*. 1995, 2003] is one such complex. It is characterized by the markedly elongate lowest basiscopic pinnules on the lowest pinna and the densely scaly petioles. Lin *et al*. (1995, 2003) recognized five species and two varieties (*D. bissetiana* (Baker) C. Chr., *D. insularis* Kodama var. *insularis*, *D. insularis* var. *chichisimensis* (Nakai ex H. Itô) H. Itô, *D. pacifica* (Nakai) Tagawa, *D. sacrosancta* Koidz., *D. saxifraga* H. Itô, and *D. varia* (L.) Kuntze). Serizawa (2009) separated *D. kobayashii* Kitag. from *D. sacrosancta* sensu lato on the basis that the former has thinner fronds and falcate pinnae. *Dryopteris protobissetiana* K. Hori et N. Murak. from Yakushima, Japan, is similar to *D. bissetiana* in having slightly bullate scales and dark green laminae, but differs in its flat, serrate margins at the apex of the upper pinnae. At present, seven species and two varieties are recognized in the *D. varia* complex.

Most species of the *D. varia* complex, such as *D. bissetiana* (Hirabayashi 1967, Nakato *et al*.

1995, Lin *et al*. 2003, Lee *et al*. 2006), *Dryopteris insularis* var. *chichisimensis* (Lin *et al*. 2003), *D. pacifica* (Hirabayashi 1970, Lin *et al*. 1992; Nakato *et al*. 1995, Lin *et al*. 2003, Lee *et al*. 2006), *D. sacrosancta* (Mitui 1965, 1968, Hirabayashi 1969, Nakato *et al*. 1995, Lin *et al*. 2003, Lee *et al*. 2006), and *D. varia* (Mitui 1966, 1968, Hirabayashi 1970, Nakato *et al*. 1995, Lin *et al*. 2003, Lee *et al*. 2006, Ebihara *et al*. 2014), are triploid apogamous (Table 1). Only two species are known to be diploid sexual; *D. saxifraga* (Hirabayashi 1967, Mitui 1975, Lee *et al*. 2006) and *D. protobissetiana* (Hori *et al*. 2014). Ebihara *et al*. (2014) recently reported that *D. varia* also has a diploid sexual cytotype in Taiwan. A few species, such as *D. bissetiana* (Hirabayashi 1966, Lee *et al*. 2006), *D. pacifica* (Lin *et al*. 1992, Nakato *et al*. 1995), and *D. varia* (Hirabayashi 1966, 1967, 1974) have been reported as having diploid cytotypes, in addition to triploid apogamous cytotypes.

Hori *et al*. (2014, in prep.) clearly showed that the classification of the apogamous species of the *D. varia* complex by Iwatsuki (1995) had issues, especially for *D. pacifica*, because three genotypes (α, β, and γ types), which have completely different genome constituents on the basis of the molecular analyses using five nuclear markers, were recognized within this species. The scientific name of *D. pacifica* (Nakai) Tagawa, based on *Polystichum pacificum* Nakai (1925) from Japan, also needs revision, since it is a later homonym of *D. pacificum* Christ (1912), a name for a Samoan species. Christ (1912) commented that *D. pacifica* was similar to *D. dissecta*, which is now placed in *Tectaria* (Xing *et al*. 2013). The separation of *D. kobayashii* from *D. sacrosancta* sensu lato (Serizawa 2009) was supported by molecular data of Hori *et al*. (2014). To classify this complex, it is important to elucidate the genetic constitution and variation within each species, especially in the apogamous species.

Recent molecular research suggested that the *Dryopteris varia* complex experienced reticulate evolution (Lee & Park 2013, Hori *et al*. 2014, in prep.) through hybridization between diploid sexual species and triploid apogamous species. The nucleotide sequences of the five nuclear markers from five diploid sexual species of the *D. varia* complex and related species were categorized in five monophyletic groups of sequences (A–E, M): A, *D. varia*; B, *D. saxifraga*; C, *D. protobissetiana*; D, *D. caudipinna*; E, *D. chinensis*; and M, *D. insularis* (only the diploid apogamous type is known from Japan). It was also shown that each triploid apogamous species of the *D. varia* complex contained two or three nucleotide sequences of the nuclear markers from two or three of the above diploid sexual species: *D. bissetiana*, B + C; *D. pacifica* (α), A + C; *D. pacifica* (β), A + B + C; *D. pacifica* (γ), A + C + D; *D. kobayashii*, B + C + E; *D. sacrosancta*, A + C + E; *D. chichisimensis*, A + C + M (Fig. 1). Therefore, these apogamous species likely underwent complicated reticulate evolution among the diploid sexual species and the triploid apogamous species. This phenomenon has led to the difficulty of identifying species in the *D. varia* complex.

In this study, the species of the *D. varia* complex in Japan were recircumscribed according to morphological characteristics, reproductive mode, chromosome number, and the genomic constitution of each species.

Materials and Methods

Observation of morphological characteristics

To classify the members of the *Dryopteris varia* complex, we first noted differences in the following morphological characteristics: size of lamina, stipe, lamina shape, color and sheen of the lamina, presence/absence of serrations on the margins of the pinnae, type shape and color of the indusia, and form of the scales. We also examined the type specimens of the species of the *D. varia* complex and sect. *Variae* in Japan and China.

Cytological observation and estimation of reproductive mode

We observed the mitotic chromosome numbers of each member of the complex. Plant materials for the cytological observation are listed in

TABLE 1. Cytotypes in the *Dryopteris varia* complex from previous study.

Taxon	Reproductive mode	Ploidy level	Chromosome number	Locality of materials	Source
D. bissetiana	apogamous	$2x$	$n = 82$	Japan	Hirabayashi (1966)
		$3x$	$n = 123$	Japan	Hirabayashi (1967), Lin *et al.* (2003)
			$2n = 123$	China	Nakato *et al.* (1995)
		$2x$, $3x$	$2n = 82, 123$	Korea	Lee *et al.* (2006)
	sexual	$4x$	$n = 82$	China	Weng (1989)
D. insularis	apogamous	$2x$	$2n = 82$	Japan	Lin *et al.* (2003)
D.chichisimensis	apogamous	$3x$	$2n = 123$	Japan	Lin *et al.* (2003)
D. pacifica	apogamous	$2x$	$n = 82$	Japan	Lin *et al.* (1992)
			$2n = 82$	Japan	Lin *et al.* (1992)
			$2n = 82$	China	Nakato *et al.* (1995)
		$3x$	$n = 123$	Japan	Hirabayashi (1970)
			$n = 123$, $2n = 123$	Japan	Lin *et al.* (1992)
			$2n = 123$	China	Nakato *et al.* (1995)
			$2n = 123$	Japan	Lin *et al.* (2003)
			$2n = 123$	Korea	Lee *et al.* (2006)
D. protobissetiana	sexual	$2x$	$2n = 82$	Japan	Hori *et al.* (2015)
D. sacrosancta	apogamous	$3x$	$n = 123$	Japan	Mitui (1965, 1968), Hirabayashi (1969)
			$2n = 123$	China	Nakato *et al.* (1995)
			$2n = 123$	Japan	Lin *et al.* (2003)
			$2n = 123$	Korea	Lee *et al.* (2006)
D. saxifraga	sexual	$2x$	$n = 41$	Japan	Hirabayashi (1967), Mitui (1975)
			$2n = 82$	Korea	Lee *et al.* (2006)
	apogamous	$3x$	$2n = 123$	Korea	Lee *et al.* (2006)
D. varia	sexual	$2x$	$2n = 82$	Tawian	Ebihara *et al.* (2014)
		$4x$	$n = 82$	Tawian	Tsai & Shieh (1975, 1985)
	apogamous	$2x$	$n = 82$	Japan	Hirabayashi (1966, 1967, 1974)
		$3x$	$n = 123$	Japan	Mitui (1966, 1968), Hirabayashi (1970)
			$2n = 123$	China	Nakato *et al.* (1995)
			$2n = 123$	Japan	Lin *et al.* (2003)
			$2n = 123$	Tawian	Ebihara *et al.* (2014)
			$2n = 123$	Korea	Lee *et al.* (2006)

Table 2. To observe mitotic chromosomes, root tips from living stocks were pretreated with 0.004-M 8-hydroxyquinoline for 7 h at approximately 15–18 °C. After fixation overnight in ethanol and acetic acid (3:1), the root tips were hydrolyzed in a mixed solution of 1N HCl and 45% acetic acid (1:1) at 60 °C for 10 min before being mashed in a 2% aceto-orcein solution. The chromosomes were observed under a Leica DM2500 microscope and then photographed using a Leica MC170 HD digital camera.

To estimate the reproductive mode of each sample or herbarium specimen, the number of spores in each sporangium were counted. We examined at least five sporangia with normal spores in each specimen. Samples with 64 spores per sporangium were estimated to be sexually reproducing; samples with 32 spores per sporangium were estimated to be apogamous (Manton 1950).

Classification with genome constitution of each species

We treated diploid sexual taxa with distinct chloroplasts and nuclear genomes as distinct species. Apogamous cytotypes with different nuclear genome constituents were also treated as independent species. *Dryopteris pacifica* (α) exhibited several genome constituents; ACC, AAC or AC. *Dryopteris bissetiana* had a BCC or B/C constitution. BBC was not recognized because of low genetic variation in *D. saxifraga* (B). However, in this study, we treated these genotypes as belonging to the same species because it was impossible to distinguish them morphologically. Autopolyploid apogamous cytotypes were treated as the same species as the diploid sexual cyto-

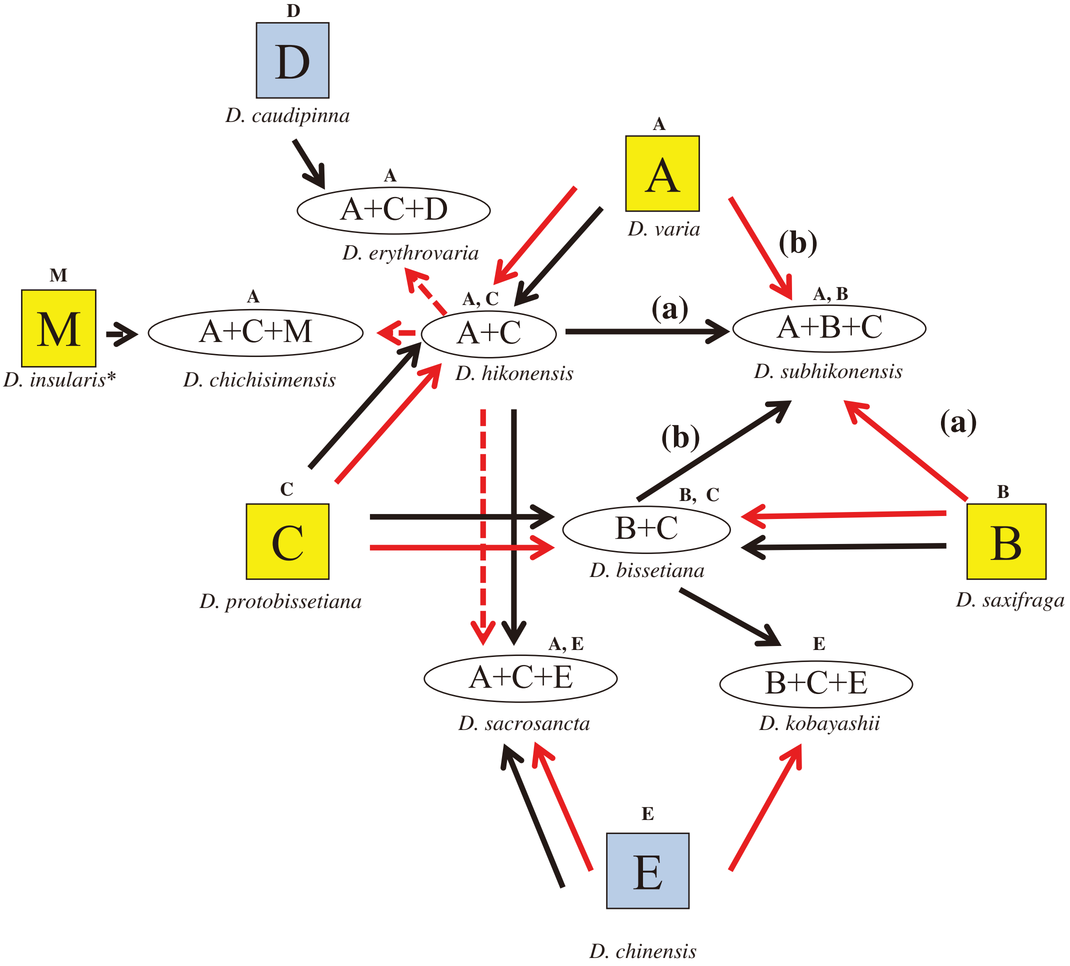


FIG. 1. Reticulogram of the *Dryopteris varia* complex and revised scientific names of each species. Yellow squares indicate diploid progenitors within the *D. varia* complex; blue squares indicate related diploid species outside of complex. Ellipses indicate apogamous species. Letters in squares and ellipses indicate genome constituents of nuclear markers. Genome constituents such as A+A+C or A+C+C, are shown as A+C. Letters above squares or ellipses indicate cpDNA genotypes. Red and black arrows indicate maternal and paternal species, respectively. Arrows with red dashes indicate apogamous maternal species. Two courses of hybridization can be supposed related to the formation of *D. subhikonensis* and are indicated as (a) and (b). *Only diploid apogamous *D. insularis* is known from Japan.

types sharing the same genome because there were no significant differences in morphological characteristics.

In this study, we examined herbarium specimens of the *Dryopteris varia* complex deposited at MAK, MBK, PE, and TNS. Voucher specimens whose genomic constituents had been fully elucidated were useful especially for describing their morphology and geographic distribution.

Results & Discussion

Cytological observation and estimation of reproductive mode

We estimated the chromosome number of the *Dryopteris varia* complex as 2*n* = 123 (apogamous) in *D. bissetiana*; 2*n* = 123 (apogamous) in *D. chichisimensis*; 2*n* = 123 (apogamous) in *D. erythrovaria* (newly reported); 2*n* = 82 (apoga-

TABLE 2. Reproductive system, ploidy level and chromosome numbers of the *Dryopteris varia* complex determined in this study.

Taxon	Reproductive mode	Ploidy level	Chromosome number	Locality	Voucher
D. bissetiana	apogamous	$2x$	$2n = 123$	Kagawa Pref.: Ayauta county, Ayagawa town	*K. Hori 532*
D. chichisimensis	apogamous	$3x$	$2n = 123$	Tokyo Pref.: Ogasawara Is. (including Kazan-retto Is.): Chichijima Is., Higashidaira	*K. Hori 1351*
D. erythrovaria (*pacifica* γ)	apogamous	$3x$	$2n = 123$	Tokyo Pref.: Inagi city, Momura	*K. Hori 485*
D. hikonensis (*pacifica* α)	apogamous	$2x$	$2n = 82$	Kagawa Pref.: Ayauta county, Ayagawa town	*K. Hori 531*
	apogamous	$3x$	$2n = 123$	Kagawa Pref.: Takamatsu city, Yashima	*K. Hori 517*
D. insularis	apogamous	$2x$	$2n = 82$	Tokyo Pref.: Ogasawara Is. (including Kazan-retto Is.): Chichijima Is., Mt. Asahiyama	*K. Hori 1350*
D. kobayashii	apogamous	$3x$	$2n = 123$	Tokyo Pref.: Inagi city, Momura	*K. Hori 8*
D. protobissetiana	sexual	$2x$	$2n = 82$	Kagoshima Pref.: (Yakushima Is).: Hann-yama	*K. Hori 1756*
D. sacrosancta	apogamous	$3x$	$2n = 123$	Saga Pref.: Takeo city, Yamauchi town	*K. Hori & Y. Inoue 490*
D. saxifraga	sexual	$2x$	$2n = 82$	Akita Pref.: Sennboku city, Dakigaeri velley	*K. Hori & Y. Horii 1494*
D. subhikonensis (*pacifica* β)	apogamous	$3x$	$2n = 123$	Tokyo Pref.: Akiruno city, Youzawa	*K. Hori 1146*
D. varia	sexual	$2x$	$2n = 82$	TAIWAN. Taipei city.: Urai	*K. Hori 1393*
	apogamous	$3x$	$2n = 123$	Saga Pref.: Kashima city	*K. Hori 495*

Key to the Japanese species of the *Dryopteris varia* complex (*Dryopteris* subg. *Erythrovariae*).

1a. Sori born only on upper part of lamina .... 5. *D. insularis*
1b. Sori born on whole lamina 2
2a. Scales deflexed .... 9. *D. saxifraga*
2b. Scales ascending 3
3a. Lamina papyraceous; center of indusia often red .... 3. *D. erythrovaria*
3b. Lamina herbaceous or coriaceous; center of indusia translucent 4
4a. Lamina herbaceous 5
4b. Lamina coriaceous 6
5a. Lamina narrowly triangular (length / width = 3/2–2/1); apex of pinnae curved, obtuse .... 6. *D. kobayashii*
5b. Lamina pentagonal (length / width = 4/3–3/2); apex of pinnae straight, acute .... 8. *D. sacrosancta*
6a. Scales on costa flat .... 11. *D. varia*
6b. Scales on costa bullate 7
7a. Scales sub-sparse on rachis; endemic to the Bonin Islands .... 2. *D. chichisimensis*
7b. Scales dense on rachis; distributed outside the Bonin Island 8
8a. Scales on upper part of petiole bullate .... 7. *D. protobissetiana*
8b. Scales on upper part of petiole flat 9
9a. Margin of apex of upper pinnae entire .... 1. *D. bissetiana*
9b. Margin of apex of upper pinnae deeply or shallowly serrate 10
10a. Margin of apex of upper pinnae deeply serrate; margin of indusia ciliate or entire .... 4. *D. hikonensis*
10b. Margin of apex of upper pinnae shallowly serrate; margin of indusia entire .... 10. *D. subhikonensis*

mous) and $2n = 123$ (apogamous) in *Dryopteris hikonensis*; $2n = 82$ (apogamous) in *D. insularis*; $2n = 123$ (apogamous) in *D. kobayashii* (newly reported); $2n = 82$ (sexual) in *D. protobissetiana*; $2n = 123$ (apogamous) in *D. sacrosancta*; $2n = 82$ (sexual) in *D. saxifraga*; $2n = 82$ (sexual) and $2n = 123$ (apogamous) in *D. varia* (Table 2).

Classification based on morphological characteristics and genome constitution of each species

We treated the taxonomy of 11 species within the *Dryopteris varia* complex: *D. bissetiana*, *D.*

chichisimensis, *Dryopteris erythrovaria* sp. nov. = *D. pacifica* (γ), *D. hikonensis* = *D. pacifica* (α), *D. insularis*, *D. kobayashii*, *D. protobissetiana*, *D. sacrosancta*, *D. saxifraga*, *D. subhikonensis* sp. nov. = *D. pacifica* (β), and *D. varia*.

Taxonomic treatment

1. **Dryopteris bissetiana** (Baker) C. Chr., Ind. Fil. 245. 1905. —Fig. 2

Nephrodium bissetianum Baker in J. Bot, 15 (180): 366. 1877. Type: Japan, Miyanoshita (presumably Kanagawa Pref.) (*J. Bisset 92*, May 24, 1876, K 442227! — holo-). — *Polystichum bissetianum* (Baker) Nakai in Bot. Mag. Tokyo 45: 102. 1931. — *Dryopteris bissetiana* var. *typica* H. Itô in Nakai et Honda, Fl. Jap. 4: 55. 1939.

Polypodium setosum Thunb., Fl. Jap. 337. 1784. Type: Japan (*Thunberg s.n.*, *UPS-THUNB 24713*— holo-). — *Aspidium setosum* (Thunb.) Sw. in Schrad. J. Bot. 1800-2: 39. 1801. — *Polystichum thunbergii* Koidz. in Bot. Mag. Tokyo 38: 106. 1924. — *Dryopteris varia* var. *setosa* (Thunb.) Ohwi, Fl. Jap. Pterid. 88: 1957. — *Dryopteris setosa* (Thunb.) Akasawa in Bull. Kochi. Wom. Univ. 7: 27. 1959. — *Dryopteris varia* subsp. *setosa* (Thunb.) Sugim., Keys Herb. Pl. Jap. Pterid. 405. 1966.

Dryopteris saxifraga H. Itô var. *deltoide*a H. Itô in Bot. Mag. Tokyo 50: 126. 1936. Type: Korea, Keikido, Koryo (*T. Nakai s.n.,* 1930, TI 13276! — holo-). — *Dryopteris saxifragivaria* Nakai in J. Jap. Bot. 18: 286. 1942. **syn. nov**.

Herbs, terrestrial, evergreen; rhizome erect, or slightly ascending. Leaves cespitose; scales dense on rhizome, petiole, rachis, and costa; petiole 10–40 cm long; scales lanceolate, ascending or deflexed, apex filiform; scales at base of petiole black, margin translucent, flat, narrow, base brown; scales on upper petiole black, flat, spreading, base brown; scales on rachis and costa black, bullate, base brown; lamina bipinnate, occasionally tripinnate at base, narrowly triangular, gradually narrowed to apex, 20–50 cm long, 10–30 cm wide, dark green or whitish green, soft coriaceous, surface shiny or dull, margins recurved; pinnae curved, apex obtuse; apical margin of pinnules entire; lowest basiscopic pinnules on lowest pinna barely longer than second lowest; sori round, medial; indusia reniform or circular, margin entire, translucent, 1.5–1.8 mm in diameter; spores per sporangium 32; chromosome number $2n = 123$ (Fig. 13a), triploid apogamous (diploid apogamous type unknown in Japan).

Notes. *Dryopteris bissetiana* is an apogamous species of hybrid origin between *D. protobissetiana* and *D. saxifraga*. It is morphologically similar to *D. protobissetiana*, *D. hikonensis*, and *D. subhikonensis*. However, *D. bissetiana* differs from them in having pinnules with an entire margin, entire indusia, and gradually narrowed lamina. It is also sometimes similar to *D. saxifraga*. Such intermediate form have been identified as *D. saxifragivaria* Nakai; however, both *D. bissetiana* and *D. saxifragivaria* are of hybrid origin between *D. protobissetiana* and *D. saxifraga*. They share the same genomes from the two diploid sexual parental species. We therefore treat them as *D. bissetiana*.

From South Korea, Lee *et al*. (2006) reported diploid apogamous *Dryopteris bissetiana*. Lee & Park (2013) reported several sequences of nuclear *PgiC* from *D. bissetiana*. However, all of their sequences nested within the clade of diploid sexual *D. saxifraga*. Their sample may not be the diploid apogamous *D. saxifraga* because its chloroplast DNA coincided with that of *D. protobissetiana*. It therefore seems possible that they failed to select the nuclear *PgiC* sequences belonging to *D. protobissetiana* from their samples of *D. bissetiana*. Only the triploid apogamous cytotype has been found in *D. bissetiana* in Japan, even though as many as 25 cytological samples have been analyzed using ploidy analysis or observations of the chromosomes.

Lee *et al*. (2006) distinguished *Dryopteris saxifragivaria* Nakai from *D. bissetiana*, because of intermediate morphological characteristics between *D. bissetiana* and *D. saxifraga*, in Korea. However, continuous morphological variation was observed between *D. bissetiana* and *D. saxifragivaria* in Japan, making it difficult to distinguish them morphologically. We conclude that they are *D. bissetiana* because they share the same genomic constitution (genomes from diploid sexual *D. saxifraga* and *D. protobissetiana*).

Weng (1989) reported a tetraploid sexual type (n = 82) of *Dryopteris bissetiana* from China, but it did not cite a voucher specimen and we are unable to confirm the identification.

Habitat and distribution. *Dryopteris bissetiana* occurs in both deciduous and broad-leaved evergreen forests and in secondary forests in Japan (Hokkaido, Honshu, Shikoku and Kyushu) (Fig. 14-1a.), Korea, and mainland China.

Japanese name. Yama-itachishida.

Specimens examined. **JAPAN.** HOKKAIDO. **Hokkaido Pref.:** Hiyama county, Esashi town, *Y. Kimizuka s.n.,* Sep. 5, 1974 (TNS). Okushiri town, Monai river, *M. Neichi s.n.,* Jul. 17 1983 (TNS). HONSHU. Aichi Pref.: Inuyama city, Tsugao, *H. Marui 2849* (TNS). **Akita Pref.:** Daisenn city, Kyouwa, *K. Hori 1453* (MAK). Aomori Pref.: Hachinohe city, Shirahama, *M. Neichi s.n.,* Oct. 5, 1980 (TNS). **Chiba Pref.:** Sakura city, *K. Hori 39* (MAK). **Fukui Pref.:** Awara city, *K. Hori 1529* (MAK). **Fukushima Pref.:** Nihonnmatsu city, Matsuoka, *H. Kobayashi s.n.,* Sep. 15 1982 (TNS). **Gifu Pref.:** Ibi county, Ibigawa town, Sakauchikawakami *T. Ogiyama 10225* (TNS). **Gunnma Pref.:** Tomioka city, Ichinomiya town, *T. Satomi s.n.,* Aug. 14, 1955 (TNS). **Hiroshima Pref.:** Hiroshima city, Asakita-ku, Asa town, *K. Hori 348* (MAK). **Hyogo Pref.:** Ashiya city, Yamaashiya town, *T. Yamada 176* (TNS). **Ibaraki Pref.:** Mt. Tsukuba, *K. Hori 636* (MAK). **Ishikawa Pref.:** Komatsu city, Kanahira town, *S. Tsugaru 13309* (TNS). **Iwate Pref.:** Shimohei county, Tanohata village, Kitayamazaki, *Y. Oda s.n.,* Oct. 18, 1981 (TNS). **Kanagawa Pref.:** Zushi city, Mt. Futago, *K. Hori 30* (MAK). **Kyoto Pref.:** Kameoka city, Asahi town, *S. Tsugaru 14749* (TNS). **Mie Pref.:** Yokkaichi city, Isaka town, *S. Yamauchi s.n.,* Sep. 21, 1980 (TNS). **Miyagi Pref.:** Igu county, Marumori town, *K. Hori 1511* (MAK). **Nagano Pref.:** Shimoina county, Yasuoka village, *M. Muramatsu 256* (TNS). **Nara Pref.:** Nara Pref., Yoshino county, *K. Hori 271* (MAK). **Niigata Pref.:** Kashiwazaki city, Yoneyama, *S. Iwano s.n.,* Sep. 26, 1965 (TNS). **Okayama Pref.:** Okayama city, Kita-ku, Ichinomiya, *K. Hori 446* (MAK). **Osaka Pref.:** Kawachinagano city, Kobuka, *H. Mitsuhashi & M. Mitsuhashi s.n.,* Jun. 28, 1982 (TNS). **Saitama Pref.:** Hannno city, *K. Hori 65* (MAK). **Shiga Pref.:** Inugami county, Taga town, *T. Tatebe s.n.,* Apr. 4, 1976 (TNS). **Shimane Pref.:** Goutsu city, Hazumi town, *H. Sawae 14493* (TNS). **Shizuoka Pref.:** Fuji city, Iwamoto, *T. Sato s.n.,* Sep. 22, 1984 (TNS). **Tochigi Pref.:** Utsunomiya city, Nozawa town, *K. Ogawa s.n.,* Mar. 20, 1957 (TNS). **Tokyo Pref.:** Nishitama county, Okutama town, *K. Inoue s.n.,* Apr. 16, 1978 (TNS). **Tottori Pref.:** Iwami county, Iwami town, *A. Tanaka s.n.,* Feb. 27, 1983 (TNS). **Toyama Pref.:** Shimoniikawa county, Asahi town, *T. Oshima s.n.,* Nov. 6, 1982 (TNS). **Yamagata Pref.:** Yonezawa city, Tateyama, *Z. Sato 3026* (TNS). **Yamaguchi Pref.:** Ube city, Kamiube, *T. Yamada s.n.,* Mar. 22, 1975 (TNS). **Yamanashi Pref.:** Minamitsuru county, *H. Endo s.n.,* Oct. 11, 1981 (TNS). **Wakayama Pref.:** Shinnguu city, *Takada H. Manago s.n.,* Dec. 12, 1971 (TNS). SHIKOKU. **Ehime Pref.:** Imabari city, Hakata town, Kitaura, *S. Hyodo 14391* (TNS). **Kagawa Pref.:** Ayauta county, Ayagawa town, *K. Hori 532* (MAK). **Kochi Pref.:** Takaoka county, Ochi town, *K. Yamaoka 31069* (TNS). **Tokushima Pref.:** Myozai county, Kamiyama town, *T. Inobe 137* (TNS). KYUSHU. **Fukuoka Pref.:** Kitakyuusyuu city, Kokuraminami-ku, *S. Kobayashi & H. Fukushima 1543* (TNS). **Kumamoto Pref.:** Kuma county, Kuma village, *T. Yamanaka s.n.,* Jan. 14, 1968 (TNS). **Kagoshima Pref.:** Yubisuki city, Mt. Kaimonndake, *T. Yamanaka s.n.,* Aug. 28, 1983 (TNS). **Miyazaki Pref.:** Nishiusuki county, Hinokage town, *Y. Akagi MZC773* (TNS). **Saga Pref.:** Imari city, Higashiyamashiro town, *Y. Tanno s.n.,* Aug. 20, 1975 (TNS). **Oita Pref.:** Hita city, Nakatsue village, *H. Tsuji oitatj-7844* (TNS). **Nagasaki Pref.:** Unnzenn city, Chijiwa town, *S. Yamada s.n.,* Sep. 6, 2012 (TNS).

2. **Dryopteris chichisimensis** Nakai ex H. Itô in Bot. Mag. Tokyo 49: 435. 1935. — Fig. 3

Type: Japan, the Bonin Islands, Chichijima, Tsutsujiyama (*T. Nakai, July 4, 1932*, TI – holo-)— *Dryopteris insularis* var. *chichisimensis* (Nakai ex H. Itô) H. Itô, Nakai et Honda, Nova Fl. Jap. 4: 57. 1939.

Herbs, terrestrial, evergreen; rhizome erect or slightly ascending. Leaves cespitose; scales dense on rhizome and costa, sub-sparse on petiole and rachis; petiole 10–40 cm long; scales lanceolate, apex filiform; scales at base of petiole black, flat, base narrow and brown; scales on upper part of petiole and rachis brown, narrow, flat at base; scales on costa brown, bullate; lamina bipinnate, occasionally tripinnate at base, widely triangular, gradually narrowed to apex, 10–30 cm long, 20–50 cm wide, dark green, soft coriaceous, surface shiny, margin flat; apex of pinnae curved; apical margin of pinnules deeply serrate; lowest basiscopic pinnules on lowest pinna slightly longer than second one; sori round, medial; indusia reniform or circular, margins ciliate, translucent, 1.5–1.8 mm in diameter; spores per sporangium 32; chromosome number $2n$ = 123 (Fig. 13b), triploid

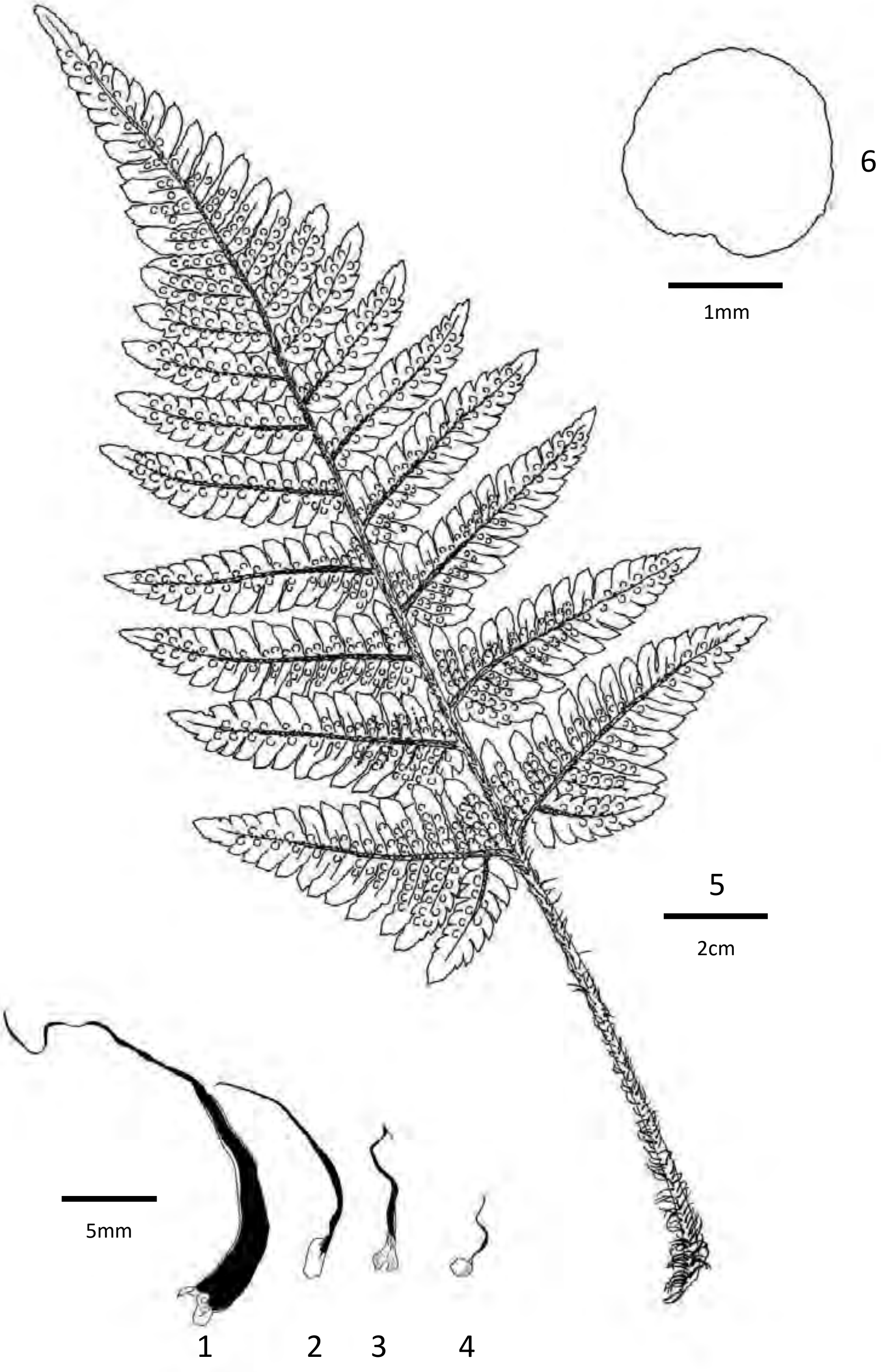


FIG. 2. *Dryopteris bissetiana* (Baker) C. Chr. 1–4: Scales at base of petiole, upper petiole, rachis and costa. 5: Frond; abaxial surface. 6: indusium. (drawn from *K. Hori 532*, MAK).

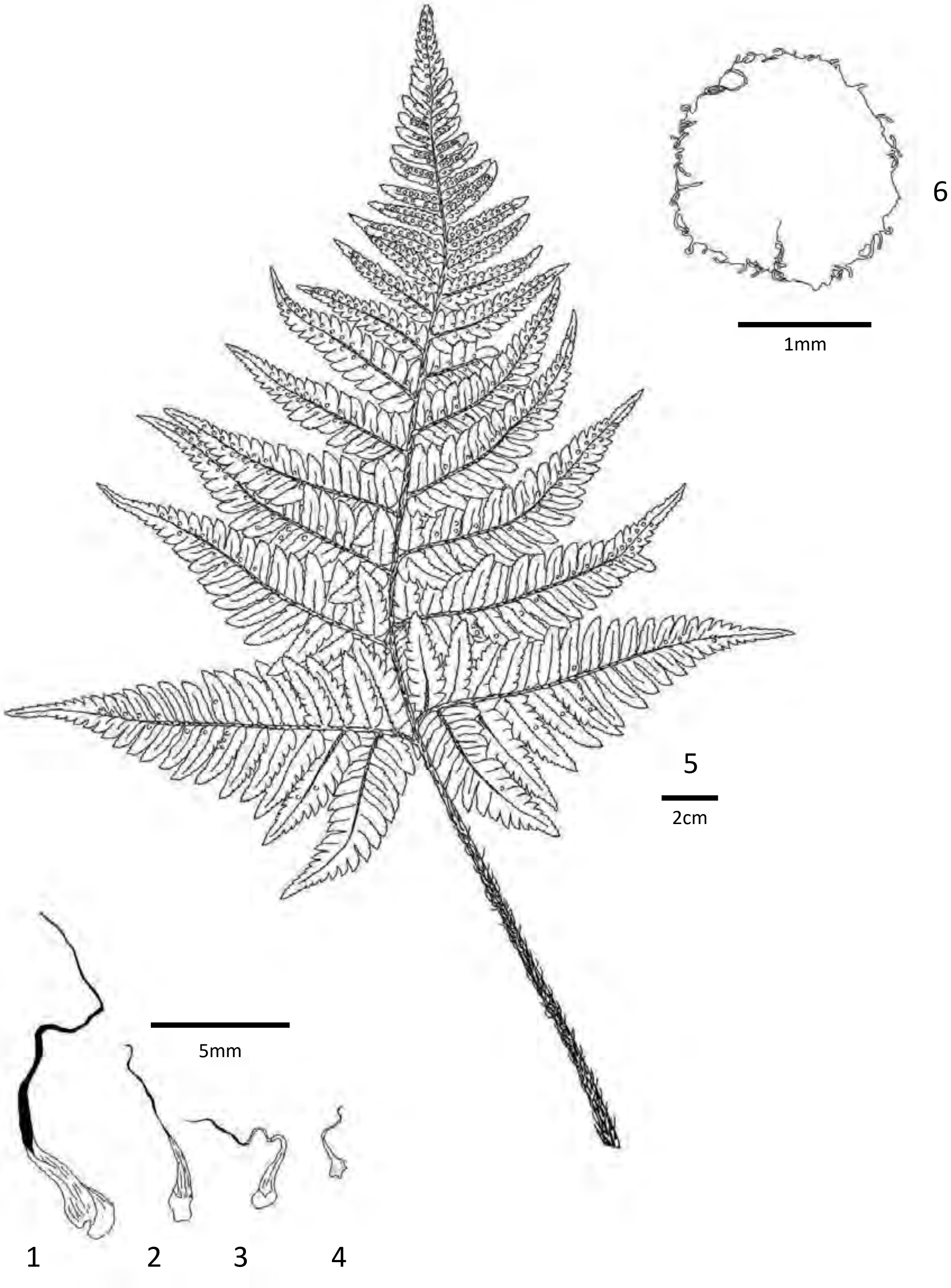


FIG. 3. *Dryopteris chichisimensis* Nakai ex H. Itô 1–4: Scales at base of petiole, upper petiole, rachis and costa. 5: Frond; abaxial surface. 6: indusium. (drawn from *K. Hori 1351*, MAK).

apogamous.

Habitat and distribution. Subtropical wet evergreen forests. Endemic to Japan (Ogasawara Islands, including Kazan-retto) (Fig. 14-1b.).

Japanese name. Chichijima-Itachishida.

Notes. *Dryopteris chichisimensis* is an apogamous species of hybrid origin between *D. hikonensis* and *D. insularis*. The parents of *D. chichisimensis* are apogamous. However, the sexual type of *D. insularis* may have existed in the past. The genome constitution of *D. chichisimensis* consists of those from *D. varia*, *D. protobissetiana* and *D. insularis*. *Dryopteris chichisimensis* is hardly distinguishable from *D. hikonensis* based only on morphological traits. It is therefore recommended that the nuclear DNA constitution be determined when reporting new localities. *Dryopteris chichishimensis* often differs from *D. hikonensis* in the sparser scales on the petiole.

Iwatsuki (1995) commented on the distribution of *Dryopteris chichishimensis* in the Izu-Islands without indicating voucher specimens. We found newly collected specimens of *D. chichisimensis* in MAK from Kita-iwoto Island in addition to specimens from Chichijima. Previous reports have cited this species as Chichijima-Benishida, its Japanese vernacular name. However, it does not have an affinity to Benishida (the *D. erythrosora complex*), but rather to Itachishida (the *D. varia* complex). Therefore, a new Japanese name, Chichijima-Itachishida is proposed here.

Specimens examined. JAPAN. **Tokyo Pref.:** Ogasawara Is. (including Kazan-retto Is.): Chichijima Is., Higashidaira, *K. Hori 1351* (MAK); Kita-iwoto *Is., T. Yasui* Jul. 10, 1993 (MAK).

3. **Dryopteris erythrovari**a K. Hori & N. Murak., **sp. nov.** — Fig. 4

Dryopteris erythrovaria K. Hori & N. Murak. is an apogamous species of hybrid origin between *D. hikonensis* and *D. caudipinna*. Its genome consists of those from *D. varia*, *D. protobissetiana*, and *D. caudipinna*. This species is characterized by the combination of large papyraceous lamina and red indusia. A large papyraceous lamina is one of the characteristics of *D. caudipinna*. Red indusia are also characteristic of *D. caudipinna*, though it sometimes has translucent indusia. The genomic constitution mentioned above may be the reason for the sometimes translucent indusia of *D. erythrovaria*, like other members of the *D. varia* complex.

Typus: Japan, Tokyo, Inagi City, Momura, approximately 100 m altitude, on soil cliff near dry road in forests, *K. Hori 2478*, collected on June 18, 2016 (holo-MAK446760).

Herbs, terrestrial, evergreen; rhizome erect or slightly ascending. Leaves cespitose; scales dense on rhizome, petiole, rachis, and costa; petiole 20–50 cm long; scales lanceolate, apex filiform; scales at base of petiole black, flat, base narrow and brown scales on upper part of petiole and rachis black, flat, base spreading and brown; scales on costa black, base bullate and brown; lamina bipinnate to tripinnatifid, widely triangular, subabruptly narrowing to apex, 30–80 cm long, 20–40 cm wide, dark green or yellowish green, papyraceous, surface shiny or dull, margin flat; pinnae straight, apex obtuse; apical margin of pinnules deeply serrate; lowest basiscopic pinnules on lowest pinna slightly longer than second lowest pinnule; sori round, medial; indusia red in center or translucent, reniform or circular, almost entire or rarely margins ciliate , 1.5–1.8 mm in diameter; spores per sporangium 32; chromosome number 2*n* = 123 (Fig. 13c), triploid apogamous.

Habitat and distribution. Warm temperate evergreen forests and secondary forests in temperate zone. Japan (Honshu, Shikoku, and Kyushu) (Fig. 14-1c.), Korea (Cheju Island) and eastern China.

Japanese name. Beni-O-Itachishida.

Specimens examined: **JAPAN.** HONSHU. **Aichi Pref.:** Atsumi county, Atsumi town, Irakomisaki, *Fukuhara 6028* (TNS). **Chiba Pref.:** Sakura city, *K. Hori 53* (MAK). **Fukui Pref.:** Imadate county, Ikeda town, Matsugaya, *Y. Saito s.n.,* Jun. 26, 1976 (TNS). **Fukushima Pref.:** Futaba county, Hirono town, *M. Yasu s.n.,* Nov. 3, 1978 (TNS). **Gifu Pref.:** Mt. Kinnkazann, *T. Nomura s.n.,* Apr. 2, 1936 (TNS). **Hiroshima Pref.:** Higashihiroshima city, *K. Hori 416* (MAK). **Hyogo Pref.:** Himeji city, Yasutomi town, Seki *T. Shiraiwa 8814* (TNS). **Ibaraki Pref.:** Iwai city, Arakyo *Y. Kimizuka s.n.,* Nov. 2, 1980 (TNS). **Kanagawa Pref.:** Kamakura city, *K. Hori 23* (MAK). **Kyoto Pref.:** Maizuru city, Nishiooura, Oohanyuu, Mt. Kunimiyama *S. Tsugaru 14839* (TNS). **Mie Pref.:** Minamimuro county, Kihou town, Ida, *K. Hori 155* (MAK). **Nara Pref.:** Takaichi county, Asuka village, Inabuchi, *Z. Tsujimoto 4762* (TNS). **Okayama Pref.:** Ihara city, Dousokei, *T. Saito s.n.,* Nov. 23, 1977 (TNS). **Osaka Pref.:** Sakai city, Ootori shrine, *T. Seto 38* (TNS). **Saitama Pref.:** Minano town, Minoyama, *T. Iwata 48713* (TNS). **Shiga Pref.:** Kouga county, Kounann town, Mt. Iwaoyama, *S. Yamauchi s.n.,* Sep. 2, 1981 (TNS). **Shimane Pref.:** Oki county, Oki Island, Nishinoshima town, Beppu, *A. Minami 39621* (TNS). **Shizuoka Pref.:** Ito city, Matsubara, *Y. Kimizuka s.n.,* Jul. 30, 1985 (TNS). **Tochigi Pref.:** Sano city, Tanuma town, *T. Waku 4555* (TNS). **Tokyo Pref.:** Inagi city, Momura, *K. Hori 2478* (MAK). **Tottori Pref.:** Yonago city, Shiroyama, *A. Tanaka s.n.,* Nov. 12, 1971 (TNS). **Wakayama Pref.:** Shinguu city, Hirokado, *Y. Kurimoto s.n.,* Dec. 27, 1930 (TNS). **Yamagata Pref.:** Yuza town, Shimo-onoso, *N. Sagawa s.n., Jul. 20, 1990* (TNS). **Yamaguchi Pref.:** Ube city, Hirose, *K. Oka 32279* (TNS). **Yamanashi Pref.:** Minamikoma county, Minobu village, Mt. Minobusann, *S. Funo 41463* (TNS). SHIKOKU. **Ehime Pref.:** Iyo county, Futami town, Houshi, *S. Hyodo s.n.,* Oct. 6, 1980 (TNS). **Kagawa Pref.:** Ayauta county, Ayanami town, Oomiya shrine, *S. Mitani 5146* (TNS). **Tokushima Pref.:** Katsuura county, Katsuura town, *C. Abe 17584* (TNS). **Kochi Pref.:** Kami county, Tosayamada town, Aburaishi, *K. Yamaoka s.n.,* Mar. 27, 1983 (TNS). KYUSHU. **Fukuoka Pref.:** Chikushino city, Futsukaichi, *N. Inoue 431* (TNS). **Kagoshima Pref.:** Aira county, Aira town, Hiramatsu, *A. Ebihara, S. Matsumoto & K. Kawahara KS2008-1628* (TNS). **Kumamoto Pref.:** Aso county, Namino village, Sakanoue, *M. Beppu 7662* (TNS). **Miyazaki Pref.:** Ebino city, Tetsuyama, *S. Tsutsui 8161* (TNS). **Nagasaki Pref.:** Iki county, Iki Island, Ashibe town, *H. Haneda s.n., May. 11, 1976* (TNS). **Oita Pref.:** Usa city, Usahachimann, *M. Nii 568* (TNS). **Saga Pref.:** Imari city, Okawauchi town, *K. Hori 485* (MAK).

CHINA. **Anhui Prov.:** She County, Mt. Qinling, *T. Nakaike 917* (TNS). **Jiangsu Prov.:** Yixing city *T. Y. Zhou 83* (PE). **Zhejiang Prov.:** Mt. Siming, *R. C. Ching 680* (PE).

KOREA. **Cheju Special Autonomous Prov.:** Cheju-do, Sop sum Island, *S. Matsumoto KR-091* (TNS).

4. **Dryopteris hikonensis** (H. Itô) Nakaike, New Fl. Jap. 841. 1992. —Fig. 5

Polystichum hololepis var. *hikonensis* H. Itô in J. Jap. Bot. 10: 451. 1934. Type: Japan, Shiga Pref. (*H. Itô, January 15, 1933,* TI — holo-). — *Dryopteris bissetiana* var. *hikonensis* (H. Itô) H. Itô in Bot. Mag. Tokyo 50: 36. 1936. — *Dryopteris varia* subsp. *hikonensis* (H. Itô) Sugim., Keys Herb. Pl. Jap. Pterid. 281, 404. 1966.

Polystichum pacificum Nakai in Bot. Mag. Tokyo 39: 119. 1925. — *Dryopteris pacifica* (Nakai) Tagawa, Col. Ill. Jap. Pterid. 211, 1959, nom. illeg., non Christ (1912).

Dryopteris immixta Ching in Fl. Tsinling. 2: 225, pl. 41, f. 1–2. 1974. **syn. nov.** Type: China, Jiangsu, Pao-hwa Shan (*C. Pei 3464,* Nov. 18, 1933, PE 44572 — holo-)

Dryopteris pudouensis Ching in Bull. Bot. Res. Harbin 3 (3): 11, f. 9. 1983. **syn. nov.** Type: China, Zhejiang, Pudou (*K. Y. Shing et al. 306,* Oct. 30, 1979, PE 44583 — holo-, PE 1895929 — iso-).

Dryopteris consimilis Ching & P. C. Chiu in Bot. Res. Academia Sinica 2: 25, t. 9, f. 3. 1987. **syn. nov.** Type: China, Zhejiang (*P. C. Chiu 510,* Jul, 1955, PE – holotype).

Dryopteris fuyangensis Ching & P. C. Chiu in Bot. Res. Academia Sinica 2: 26, t. 9, f. 4. 1987. **syn. nov.** Type: China, Zhejiang (*P. C. Chiu 4413,* Sep, 1973, PE – holo-).

Dryopteris lungjingensis Ching & P. C. Chiu [*"luntsingensis"*] in Bot. Res. Academia Sinica 2: 27, pl. 10. 1987. **syn. nov.** Type: China, Zhejiang, Hangchou, Lungjing (*P. C. Chiu 3477,* PE — holo-).

Dryopteris paravaria Ching & P. C. Chiu in Bot. Res. Academia Sinica 2: 22, t. 8, f. 3. 1987. **syn. nov.** Type: China, Guangxi, Lung-sheng Xian (*P. C. Chiu 4686,* PE1863774 — holo-, PE 1863775 — iso-).

Dryopteris shanghaiensis Ching & P. C. Chiu in Bot. Res. Academia Sinica 2: 24, t. 9, f. 1. 1987. **syn. nov.** Type: China, Shanghai, She Shan (*P. C. Chiu 4445,* July 17, 1973, PE 1863769 — holo-).

Dryopteris tieanzuensis Ching & P. C. Chiu in Bot. Res. Academia Sinica 2: 24, t. 9, f. 2. 1987. **syn. nov.** Type: China, Zhajiang, Hangzhou, Tien-tso (*P. C. Chiu 3555,* Nov 15, 1967, PE — holo-)

Dryopteris yushanensis Ching & P. C. Chiu in Bot. Res. Academia Sinica 2: 28, t. 10, f. 2. 1987. **syn. nov.** Type: China, Zhajiang, Fu-yang, Yü-shan (P. *C. Chiu 4486,* PE — holo-)

Dryopteris quadrifida Ching ex K.H.Shing & J. F. Cheng in Jiangxi Sci. 8 (3): 49. 1990. **syn. nov.** Type: China, Jiangxi, Mt. Wugong (*The Jiangxi Group 1161,* Sept. 9, 1959, PE 1863701 — holo-).

Herbs, terrestrial, evergreen; rhizome erect or slightly ascending. Leaves cespitose; scales on rhizome, petiole, rachis and costa dense; petiole 10–40 cm long; scales lanceolate, ascending, apex filiform; scales at base of petiole, upper petiole, and rachis black to blackish brown, flat, base

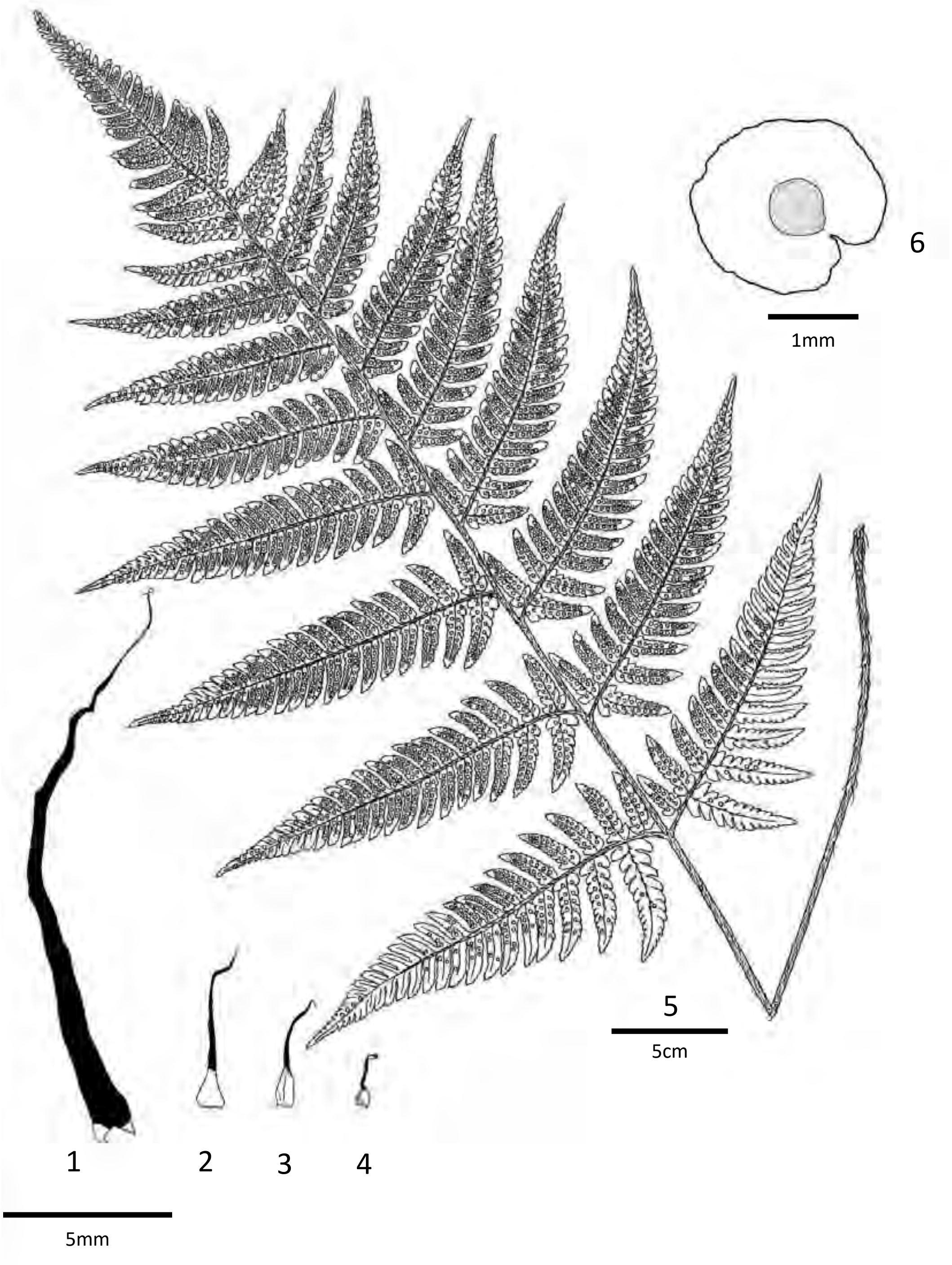


FIG. 4. *Dryopteris erythrovaria* K. Hori & N. Murak. 1-4: Scales at base of petiole, upper petiole, rachis and costa. 5: Frond; abaxial surface. 6: indusium. (drawn from type specimen, *K. Hori 2478*, MAK).

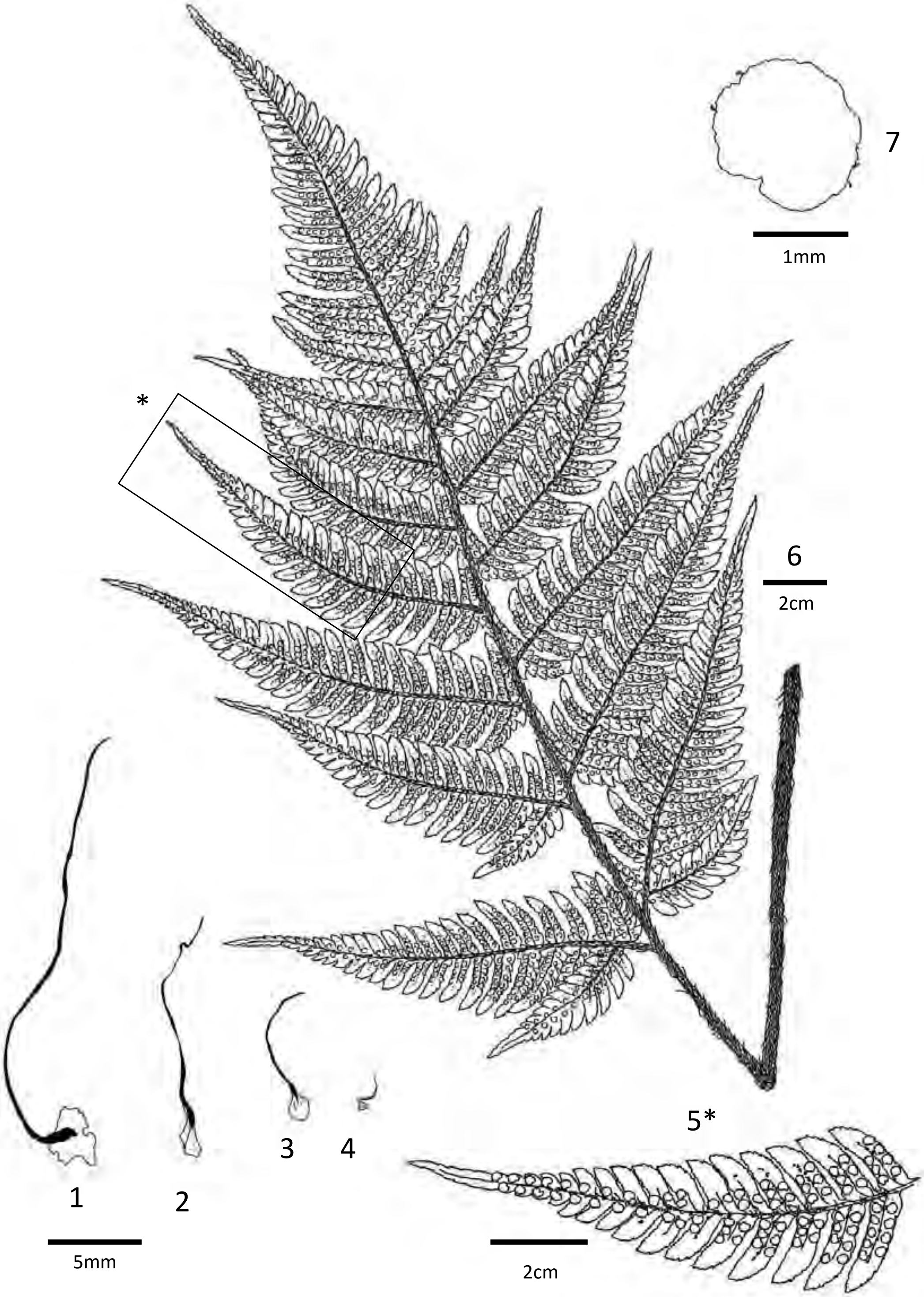


Fig. 5. *Dryopteris hikonensis* (H. Itô) Nakaike 1–4: Scales at base of petiole, upper petiole, rachis and costa. 5: Frond; abaxial surface of upper pinnae. 6: abaxial surface. 7: indusium. (drawn from *K. Hori 647*, MAK).

spreading and brown; scales on costa brown, bullate; lamina bipinnate, occasionally tripinnate at base, widely triangular, sub-abruptly narrowing to apex, 20–50 cm long, 10–30 cm wide, dark, yellowish or whitish green, soft coriaceous, surface shiny or dull, margin flat; pinnae curved, apex acute; apical margins of pinnules deeply serrate; lowest basiscopic pinnule on lowest pinna slightly longer than second lowest pinnule; sori round, medial; indusia reniform or circular, entire or margins ciliate, translucent, 1.5–1.8 mm in diameter; spores per sporangium 32; chromosome number $2n = 82$ (diploid apogamous, Fig. 13d) or $2n = 123$ (triploid apogamous, Fig. 13e).

Habitat and distribution. Warm temperate to subtropical evergreen forests and secondary forests in temperate to subtropical zones. Japan (Honshu, Shikoku, Kyushu and Ryukyu) (Fig. 14-1d.), Korea, and eastern China.

Japanese name. O-Itachishida.

Notes. *Dryopteris hikonensis* is an apogamous species of hybrid origin between *D. varia* and *D. protobissetiana*. It differs from *D. varia* in having slightly bullate scales on the rachis and from *D. protobissetiana* in having flat scales on the petiole and lowest basiscopic pinnules on the lowest pinna slightly longer than second basiscopic pinnule.

Dryopteris lungjingensis, *D. pudouensis*, *D. quadrifida* and *D. yushanensis* are treated as synonyms of *D. pacifica* by Zhang *et al*. (2013), based on morphological similarities. However, we treat them as synonyms of *D. hikonensis* in this study because *D. pacifica* is an illegitimate later homonym. In Zhang *et al*. (2013), *D. consimilis* and *D. fuyangensis* are treated as synonyms of *D. varia*; *D. paravaria* and *D. shanghaiensis* are treated as synonyms of *D. setosa*; and *D. tieanzuensis* is treated as a synonym of *D. sacrosancta*. These names can be regarded as synonyms of *D. hikonensis* based on morphological similarities. In addition, *D. immixta* (triploid apogamous species, Weng 1989) can also be regarded as a synonym of *D. hikonensis*. Genome constituents of the members of the *D. varia* complex in China still need to be clarified.

Specimens examined: **JAPAN.** HONSHU. **Aichi Pref.:** Okazaki city, Iwato town, *K. Inukai 2908* (TNS). **Chiba Pref.:** Chiba city, *K. Hori 696* (MAK). **Fukui Pref.:** Obama city, Wakasa, *S. Watanabe s.n.,* Sep. 3, 1978 (TNS). **Fukushima Pref.:** Iwaki city, Yoshima town, *M. Yasu s.n.,* Oct. 26, 1980 (TNS). **Gifu Pref.:** Annpachi county, Wanouchi town, Sato, *Y. Yamamoto s.n.*, Nov. 24, 1979 (TNS). **Hiroshima Pref.:** Kure city, Mt. Yasumi, *K. Hori 425* (MAK). **Hyogo Pref.:** Ashiya city, Kouza fall, *T. Shiraiwa 8043* (TNS). **Ibaraki Pref.:** Inashiki county, Miura village, *M. Yasu s.n.,* Dec. 28, 1974 (TNS). **Ishikawa Pref.:** Hakui county, Shika town, Yaguradani, *S. Komaki s.n.,* Aug. 25, 1975 (TNS). **Kanagawa Pref.:** Yokosuka city, Nagaura town, *T. Sato s.n.,* Oct. 6, 1974 (TNS). **Kyoto Pref.:** Miyazu city, Hioki, *T. Nakaike s.n.,* Jun. 6, 1982 (TNS). **Mie Pref.:** Kumano city, Atashika town, Atashika, *K. Oohora s.n.*, Mar. 8, 1981 (TNS). Nagano Pref.: Shimoina county, Yasuoka village, Tamoto, *H. Tsutsumi s.n.*, Mar. 31, 1981 (TNS). **Nara Pref.:** Uda county, Soni village, Kake, *Y. Kimizuka s.n.*, Jun. 11, 1979 (TNS). **Okayama Pref.:** Okayama city, Kita-ku, Ichinomiya, *K. Hori 447* (MAK). **Osaka Pref.:** Kawachinagano city, Kannshinn temple, *A. Komaki s.n.,* Aug. 29, 1982 (TNS). **Saitama Pref.:** Hannno city, *K. Hori 67* (MAK). **Shiga Pref.:** Maibara city, *K. Hori 257* (MAK). **Shimane Pref.:** Oki county, Oki Island, Nishinoshima town, *H. Endo s.n.*, Aug. 4, 1981 (TNS). **Shizuoka Pref.:** Haibara county, *K. Hori 286* (MAK). **Tochigi Pref.:** Ashikaga city, Tsukiya town, *T. Noguchi, H. Ogura & Y. Tamura s.n.*, Sep. 6, 1987 (TNS). **Tokyo Pref.:** Minato Ward, Shiba, *Y. Kimizuka s.n.,* Aug. 14, 1981 (TNS). **Tottori Pref.:** Iwami county, Iwami town, *A. Tanaka s.n.,* Dec. 26, 1981 (TNS). **Toyama Pref.:** Shimoshinnkawa county, Asahi town, Oohira, *T. Oshima s.n.,* Oct. 1, 1983 (TNS). **Wakayama Pref.:** Ito county, Katsuragi town, Hoshikawa, *H. Manago s.n.*, May. 7, 1978 (TNS). **Yamaguchi Pref.:** Shimomatsu city, Kawachiyoshiwara, *H. Masaki s.n.,* Dec. 28, 1989 (TNS). *Yamanashi Pref.:* Ootsuki city, Sasago town, Hunahashisawa, *A. Yamamoto s.n.,* Aug. 18, 1981 (TNS). SHIKOKU. **Ehime Pref.:** Iyo city, Futami town, Kaminada, *S. Hyodo 13514* (TNS). **Kagawa Pref.:** Takamatsu city, Yashima, *K. Hori 517* (MAK); Ayauta county, Ayagawa town, *K. Hori 531* (MAK). **Kochi Pref.:** Aki county, Kitagawa village, Nishinotani, *Y. Yamamoto 1231* (TNS). **Tokushima Pref.:** Anann city, Suii town, *T. Nakayama s.n.*, Aug. 2, 1979 (TNS). KYUSHU. **Fukuoka Pref.:** Onnga county, Ashiya town, Yamaga, T. *Kimura s.n.*, May. 16, 1982 (TNS). **Kagoshima Pref.:** Kumage county, Yakushima Is., Kurio, *T. Nakaike s.n.*, Aug. 18, 1982 (TNS). **Kumamoto Pref.:** Yatsushiro city, Izumi town, *K. Hori 647* (MAK). **Miyazaki Pref.:** Nobeoka city, Uwada town, *T. Minamitani 33567* (TNS). **Nagasaki Pref.:** Iki county, Ashibe town, Moroyoshi, Nakafure, *S. Tsutsui 19724* (TNS). **Ooita Pref.:** Kitsuki city, Funabe, *Y. Takaoka s.n.*, Jun. 29, 1978 (TNS). **Saga Pref.:** Imari city, Imari town, *Y. Kuranari s.n.*, Nov. 15, 1981 (TNS). RYUKYU. **Okinawa Pref.:** Naha city, Syuri, Mt. Benngatake, *M. Takara & T. Takara s.n.*, Jul. 9, 1977 (TNS).

CHINA. **Jiangxi Prov.:** Yu Shan city, Mt. Huai, *M. X. Nie 6442* (PE). **Zhejiang Prov.:** Hangzhou city, *R. C. Ching 1643* (PE).

KOREA. **Cheju Special Autonomous Prov.:** Cheju-do, Sop sum Island, *S. Matsumoto KR-067* (TNS).

5. **Dryopteris insularis** Kodama, Icon. Pl. Koisik. 2: t. 49. 1914.—Fig. 6

Type: Japan (the Bonin Islands, Tokyo Pref.) (TI – holo-). — *Dryopteris insularis* var. *typica* H. Itô in Nakai & Honda, Nova Fl. Jap. 4: 57. 1939. — *Dryopteris varia* var. *insularis* (Kodama) H. Ohba in Sci. Rep. Tohoku Univ. B 36: 113. 1971.

Herbs, terrestrial, evergreen; rhizome erect or slightly ascending. Leaves cespitose; scales dense on rhizome and costa, sub-sparse on petiole and rachis; petiole 20–35 cm long; scales brown, lanceolate, ascending, apex filiform; base of scales at base of petiole, upper petiole, and rachis flat, narrow; base of scales on costa bullate; lamina bipinnate to tripinnatifid, widely triangular, gradually narrowing to apex, 35–45 cm long, 25–35 cm wide, yellowish green, soft coriaceous, surface shiny, margin flat; pinnae straight, apex obtuse; pinnules obtuse, apical margin finely serrate; lowest basiscopic pinnules on lowest pinna barely longer than second lowest pinna; sori round, borne on upper part of lamina, sori-bearing pinnae contracted; sori round, medial; indusia reniform, glandular, margins ciliate, translucent, approximately 1.5–1.8 mm in diameter; spores per sporangium 32; chromosome number $2n = 82$, diploid apogamous (Fig. 13f).

Habitat and distribution. Subtropical dry evergreen forests. Endemic to Japan (Bonin Islands) (Fig. 14-1e.).

Japanese name. Munin-Itachishida.

Notes. Dryopteris insularis is characterized by having sori borne only on the upper part of the lamina and indusia with glandular ciliate margins. Its genome differs from other sexual species and apogamous species.

In previous studies, *D. insularis* cited as Munin-Benishida. However, as indicated for *D. chichisimensis*, it has no affinity with Benishida (the *D. erythrosora* complex), but instead definitely belongs to the Itachishida group (the *D. varia* complex). Thus, the new Japanese name, Munin-Itachishida, is proposed here.

Specimens examined. JAPAN. **Tokyo Pref.:** Ogasawara Is. (including Kazan-retto): Chichijima, Asahiyama, *K. Hori 1350* (MAK); Hahajima, Chibusayama, *M. Ito, H. Setoguchi, M. Nakazawa, H. Ishikawa. Mar. 19, 1994* (MAK).

6. **Dryopteris kobayashii** Kitag., Rep. First Sci. Exped. Manchoukuo 4 (2): 56, f. 11. 1935. — Fig. 7

Type: China, Fengtian, Hsiao-ping-tao. (*M. Kobayashi 39.* October 9, 1932, TI).

Herbs, terrestrial, evergreen; rhizome erect or slightly ascending. Leaves cespitose; scales dense on rhizome, sparse on petiole, rachis and costa; petiole 10–40 cm long; scales lanceolate, apex filiform; scales at base of petiole black, margin translucent, base flat, narrow and brown, scales on upper petiole black, flat, narrow, base brown; scales on rachis black, flat, spreading, base brown; scales on costa brown, bullate; lamina bipinnate to tripinnatifid, narrowly triangular, gradually narrowing to apex, 20–40 cm long, 10–20 cm wide, yellowish green, herbaceous, surface dull, margin flat; pinnae curved, apex obtuse; pinnules entire or shallowly serrate or apical margin serrate; lowest basiscopic pinnules on lowest pinna barely longer than second basiscopic pinnule; sori round, medial; indusia translucent, reniform or circular, margins entire, translucent, 1.5–1.8 mm in diameter; spores per sporangium 32; chromosome number $2n = 123$ (Fig. 13g), triploid apogamous.

Habitat and distribution. Warm temperate ev-

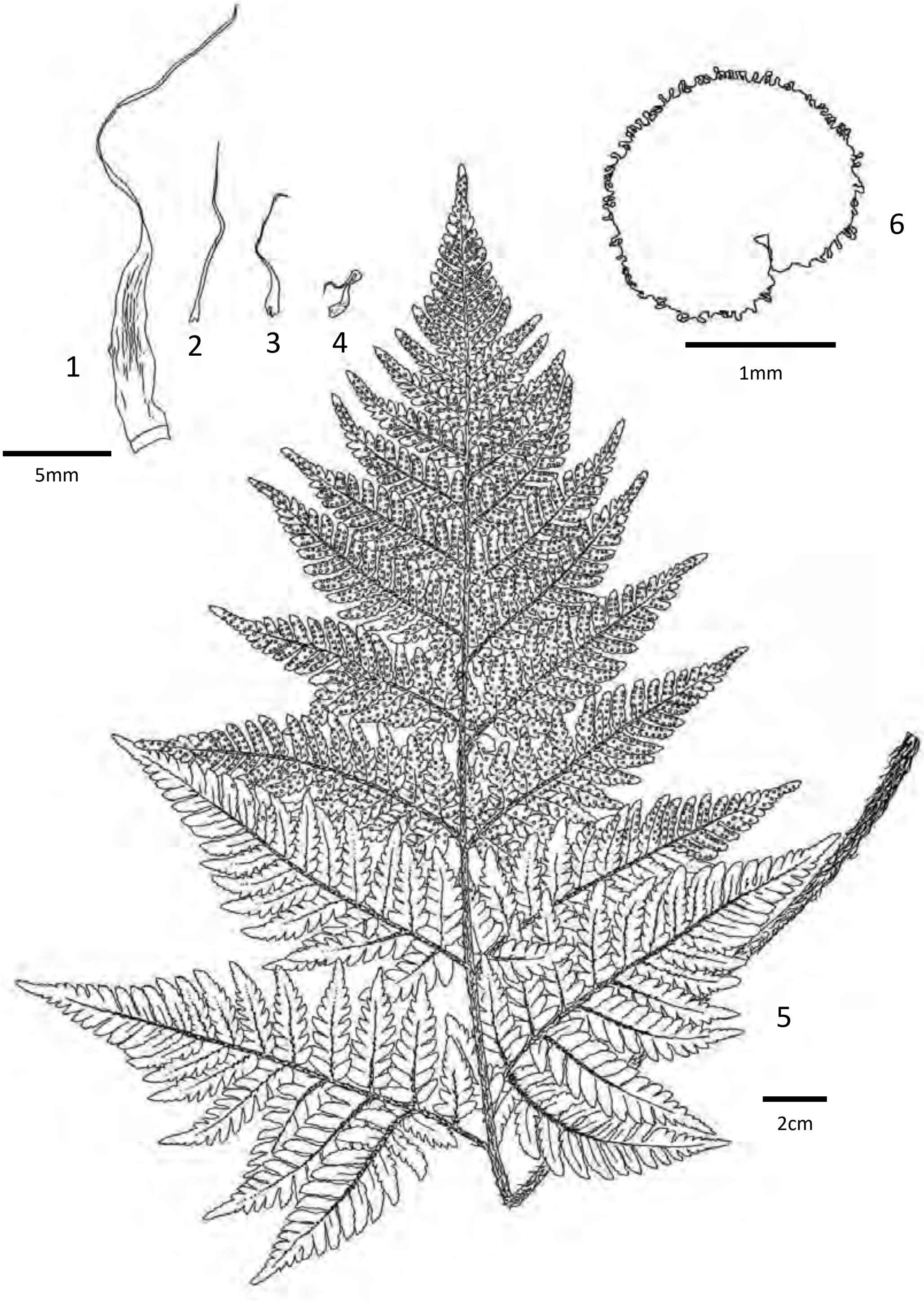


FIG. 6. *Dryopteris insularis* Kodama 1–4: Scales at base of petiole, upper petiole, rachis and costa. 5: Frond; abaxial surface. 6: indusium. (drawn from *K. Hori 1350*, MAK).

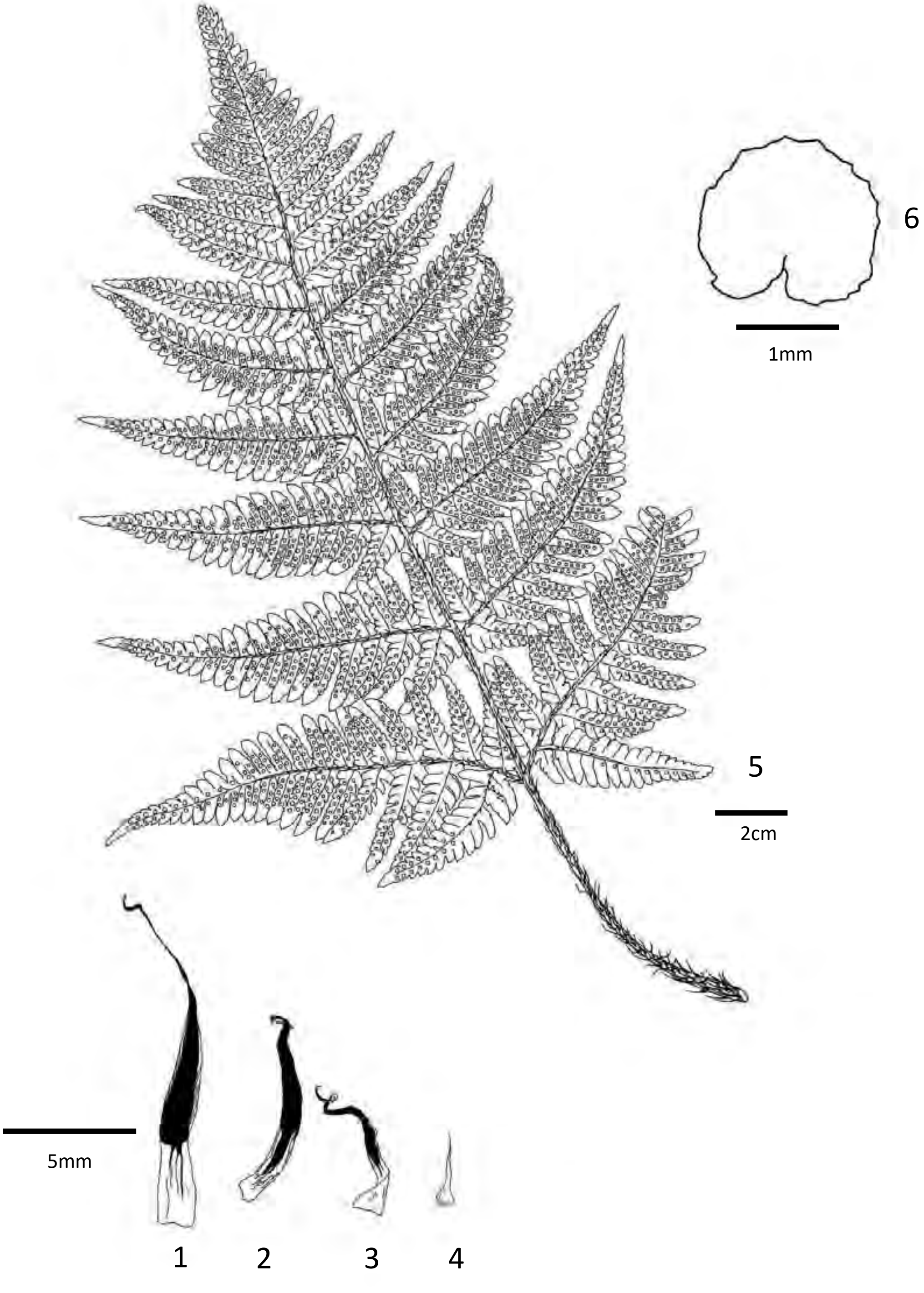


FIG. 7. *Dryopteris kobayashii* Kitag. 1–4: Scales at base of petiole, upper petiole, rachis and costa. 5: Frond; abaxial surface. 6: indusium. (drawn from *K. Hori 8*, MAK).

ergreen forests and secondary forests in temperate zone. Japan (Honshu, Shikoku, and Kyushu) (Fig. 14-1f.), Korea, and eastern China.

Japanese name. Ryoto-Itachishida.

Notes. *Dryopteris kobayashii* is an apogamous species of hybrid origin between *D. bissetiana* and *D. chinensis*. Its genome comprises those from *D. saxifraga*, *D. protobissetiana* and *D. chinensis*. *Dryopteris kobayashii* is similar in gross morphology to *D. sacrosancta*, but is distinguishable by its narrowly triangular lamina, curved pinnae with an obtuse apex and always whitish green young pinnules.

Specimens examined. **JAPAN.** HONSHU. **Aichi Pref.:** Higashikamo county, Asuke town *K. Inukai 9096* (TNS). **Chiba Pref.:** Sakura city, Odake, *K. Hori 247* (MAK). **Fukushima Pref.:** Futaba county, Namie town, *T. Waku s.n.,* Dec. 6, 1979 (TNS). **Gifu Pref.:** Ena county, Yamaoka town, *Y. Yamamoto s.n.*, Sep. 18, 1974 (TNS). **Gunnma Pref.:** Hokuchi village, Shimohakoda, *T. Wakana s.n.*, Jul. 10, 1955 (TNS). **Hiroshima Pref.:** Yamagata county, Geihoku town, *T. Takeda 10035* (TNS). **Hyogo Pref.:** Koube city, Mt. Maya, *M. Inada 1054* (TNS). **Ibaraki Pref.:** Moriya city, *K. Hori 1176* (MAK). **Kanagawa Pref.:** Kawasaki city, Asao, *K. Hori 224* (MAK). **Miyagi Pref.:** Higashimatsushima city, Miyatojima Island, *M. Adachi & Y. Adachi 59* (TNS). **Nagano Pref.:** Iida city, Imamiya shrine, *T. Nagai s.n.*, Jun. 2, 1970 (TNS). **Nara Pref.:** Yoshino county, Tennkawa village, *F. Kasetani 664N-1* (TNS). **Osaka Pref.:** Minamikawachi county, Chihaya, *I. Yamazumi IY025* (TNS). **Saitama Pref.:** Chichibu city, Urayama, *T. Iwata 11456* (TNS). **Shiga Pref.:** Otsu city, Sakamoto, *T. Waku 4884* (TNS). **Shimane Pref.:** Ouchi county, Yamato village, *N. Kurosaki 22237* (TNS). **Shizuoka Pref.:** Fujinomiya city, Nebara, *T. Sato 8640* (TNS). **Tochigi Pref.:** Sano city, Mt. Karasawa, *T. Waku 6881* (TNS). **Tokyo Pref.:** Inagi city, Momura, *K. Hori 8* (MAK). **Yamanashi Pref.:** Minamikoma county, Hayakawa town, *M. Nakagawa s.n.*, Oct. 24, 1981 (TNS). **Yamagata Pref.:** Akumi county, Yusa town, *M. Kato 8117* (TNS). SHIKOKU. **Kochi Pref.:** Agawa county, Ikekawa village, *Y. Yamamoto 37424* (MBK). KYUSHU. **Oita Pref.:** Kokonoe town, Takigami, *M. Ishizuka s.n.*, Oct. 24 1976 (TNS). **Saga Pref.:** Fujitsu county, Tara town, *H. Koike s.n.*, Nov. 16, 1975 (TNS).

CHINA. **Shandong Prov.:** Mt. Kunyu *J. X. Li 97* (PE).

KOREA. **Hong dao.:** *X. C. Zhang 3673* (PE).

7. **Dryopteris protobissetiana** K. Hori et N. Murak. in Acta Phytotax. Geobot. 66: 47–57, 2015. —Fig. 8

Type: Japan, Kagoshima Pref., Yakushima, Mt. Myojo, 300 m alt, *K. Hori 913* (holo-, MAK).

Herbs, terrestrial, evergreen; rhizome erect or slightly ascending. Leaves cespitose; scales dense on rhizome, petiole, rachis, and costa; petiole 10–30 cm long; scales at base of petiole black, flat, spreading, base brown; scales on upper petiole black, base brown, bullate; scales on rachis and costa brown, bullate; lamina bipinnate, occasionally tripinnate at base, narrowly triangular, gradually narrowing to apex, 10–40 cm long, 10–20 cm wide, dark green, soft coriaceous, surface shiny, margin flat; pinnae straight, apex obtuse; apical margin of pinnules finely serrate; lowest basiscopic pinnules on lowest pinna barely longer than second basiscopic pinnule; sori round, medial or relatively nearer to margin than to midrib; indusia reniform or circular, margins entire or erose, translucent, approximately 1.5–1.8 mm in diameter; spores per sporangium 64; chromosome number $2n = 82$ (Fig. 13h) diploid sexual.

Habitat and distribution. Warm temperate evergreen forests. Japan (southern part of Yakushima, Kagoshima Pref., Kyushu) (Fig. 14-2g.).

Japanese name. Moto-Itachishida.

Notes. *Dryopteris protobissetiana* is most similar to *D. bissetiana* in having slightly bullate scales and a dark green lamina surface, but differs from it in having flat, serrate margins at the apexes of the upper pinnae and flat margins of the lamina.

Specimens examined. **JAPAN.** KYUSHU. **Kagoshima Pref. (Yakushima).:** Hanaage river, *T. Nakaike s.n.*, Aug. 17, 1982 (TNS); Hann-yama, *K. Hori 1756* (MAK); Kawahara, *K. Hori 1836* (MAK); Koshima, *S. Tagane TF269* (TNS); Koyouji, *K. Hori 1863* (MAK); Mt. Mocchomu-dake, *K. Hori 917* (MAK); Mt. Myojo, *K. Hori 906* (MAK), *K. Hori 913* (MAK); Nakabase, *K. Hori 1851* (MAK); O-ko, *K. Hori 1872* (MAK); Yudomari, *T. Oka & K. Hori 1344* (MAK).

8. **Dryopteris sacrosancta** Koidz. in Bot. Mag. Tokyo 38: 108. 1924.—Fig.9

Type: Japan, Hiroshima Pref., Miyajima. (*Faurie s.n*., November 1913, KYO – lecto- designated by Tagawa, Acta Phytotax. Geobot. 16: 183. 1956). — *Polystichum sacrosanctum* (Koidz.) Koidz. in Bot. Mag. Tokyo 43: 388. 1929. — *Polystichum bissetianum* var. *sacrosanctum* (Koidz.) Nakai in Bot. Mag. Tokyo 45: 103. 1931. — *Dryopteris bissetiana* var. *sacrosancta* (Koidz.) H. Itô in Bot. Mag. Tokyo 50: 36. 1936. — *Dryopteris varia* var. *sacrosancta* (Koidz.) Ohwi in Fl. Jap. Pterid. 88. 1957. — *Dryopteris varia* subsp. *sacrosancta* (Koidz.) Sugim., Keys Herb. Pl. Jap. Pterid. 281. 405. 1966.

Dryopteris bissetiana var. *tenerifrons* H. Itô in Bot. Mag. Tokyo 50: 37. 1936. Type: Japan, Prov. Aki (Hiroshima Prefecture), Miyazima (*U. Faurie 444*, TI – holo-).

Herbs, terrestrial, evergreen; rhizome erect or slightly ascending. Leaves cespitose; scales dense on rhizome, sparse on petiole, rachis, and costa; petiole 10–40 cm long; scales lanceolate, apex filiform; scales at base of petiole black, margin translucent, flat, spreading, base brown; scales on upper petiole, rachis, and costa black, flat, spreading, base brown; lamina bipinnate to tripinnatifid, pentagonal, sub-abruptly narrowing to apex, 20–50 cm long, 10–30 cm wide, yellowish green, herbaceous, surface weakly shiny or dull, margin flat; pinnae straight, apex acute; apical margins of pinnules finely serrate; lowest basiscopic pinnules on lowest pinna slightly longer than second basiscopic pinnule; sori round, medial; indusia translucent, reniform or circular, margins entire, translucent, 1.5–1.8 mm in diameter; spores per sporangium 32; chromosome number $2n = 123$ (Fig. 13i), triploid apogamous.

Habitat and distribution. Warm temperate evergreen forests. Endemic to Japan (Honshu, Shikoku and Kyushu) (Fig. 14-2h.).

Japanese name. Hime-Itachishida.

Notes. *Dryopteris sacrosancta* is an apogamous species of hybrid origin between *D. hikonensis* and *D. chinensis*. Its genome consists of those from *D. varia*, *D. protobissetiana* and *D. chinensis*. *Dryopteris sacrosancta* and *D. kobayashii* are similar in having herbaceous, yellowish green lamina. The scales of these two species are sparser than in other members of the *D. varia* complex. However, *D. sacrosancta* is distinguished from *D. kobayashii* by having widely triangular lamina, pinnae with a straight, acute apex, and sometimes reddish brown young pinnules.

Specimens examined. **JAPAN.** HONSHU. **Aichi Pref.:** Gamagoori city, Sagara town, *M. Fukuhara s.n*., Nov. 17, 1976 (TNS). **Chiba Pref.:** Sakura city, *K. Hori 41* (MAK). **Hiroshima Pref.:** Hatsukaichi city, *K. Hori 305* (MAK). **Hyogo Pref.:** Kasai city, Kawachi town, *T. Shiraiwa s.n*., May. 20, 1978 (TNS). **Ibaraki Pref.:** Ishioka city, Takahama, *T. Waku s.n*., Nov. 15, 1976 (TNS). **Kanagawa Pref.:** Ashigarashimo county, Manazuru town, *T. Kawasaki 5058* (TNS). **Kyoto Pref.:** Kyoto city, Sakyo-ku, *N. Yoshikawa 1742* (TNS). **Mie Pref.:** Kumano city, Hadasu, *K. Hori 164* (MAK). **Nagano Pref.:** Shimoina county, Anann town, *F. Konta & J. Kitagawa s.n*., Sep. 6, 2010 (TNS). **Nara Pref.:** Yoshino county, Totsugawa village, *K. Kawabata 12135* (TNS). **Okayama Pref.:** Kasaoka city, Ooshima, *I. Akasawa 217* (TNS). **Osaka Pref.:** Minoo city, Minoo park, *T. Oka s.n*., Mar. 28, 1974 (TNS). **Shimane Pref.:** Izumo city, Nishihayashigi town, *M. Yagiura 7587* (TNS). **Shizuoka Pref.:** Haibara county, *K. Hori 282* (MAK). **Tochigi Pref.:** Ootawara city, Fukuhara town, *K. Ogawa s.n*., Sep. 22, 1957 (TNS). **Tokyo Pref.:** Hachioji city, Kamikawa town, Mt. Imaguma, *T. Sato 5599* (TNS). **Tottori Pref.:** Tottori city, Yoshioka, *A. Tanaka s.n*., Dec. 25, 1962 (TNS). **Wakayama Pref.:** Shinnguu city, Takada, *K. Ohora 20594* (TNS). **Yamaguchi Pref.:** Yanai city, Heigunn, *H. Masaki s.n*., Aug. 11, 1976 (TNS). **Yamanashi Pref.:** Minamikoma county, Uchibuna, H. Obata, *M. Mase & M. Takahashi s.n*., Nov. 23, 1985 (TNS). SHIKOKU. **Ehime Pref.:** Uwajima city, Tojima, *Y. Kimizuka 1223562* (TNS). **Kagawa Pref.:** Takamatsu city, Yashima, *K. Hori 262*, (MAK). **Kochi Pref.:** Kochi city, Fudeyama, *K. Nishimura*, *N. Inagaki & N. Tanaka 20171* (TNS). **Tokushima Pref.:** Itano county, *K. Hori 408* (MAK). KYUSHU. **Fukuoka Pref.:** Buzenn city, Iwaya, *S. Tsutsui 6373* (TNS). **Kagoshima Pref.:** Imizu city, Kamiokawauchi, *T. Yamanaka s.n*., Feb. 22, 1963 (TNS). **Kumamoto Pref.:** Kuma county, Mizukami village, *M. Beppu 1145* (TNS). **Miyazaki Pref.:** Nobeoka city, Daikyou river, *A. Minami & U. Fujiyama 51218* (TNS). **Nagasaki Pref.:** Shimabara city, Shiratani, *S. Tsutsui 15193* (TNS). **Oita Pref.:** Saiki city, Kariu, *M. Hadano s.n*., Sep. 5, 1976 (TNS). **Saga Pref.:** Takeo city, Yamauchi town, *K. Hori & Y. Inoue 490* (MAK).

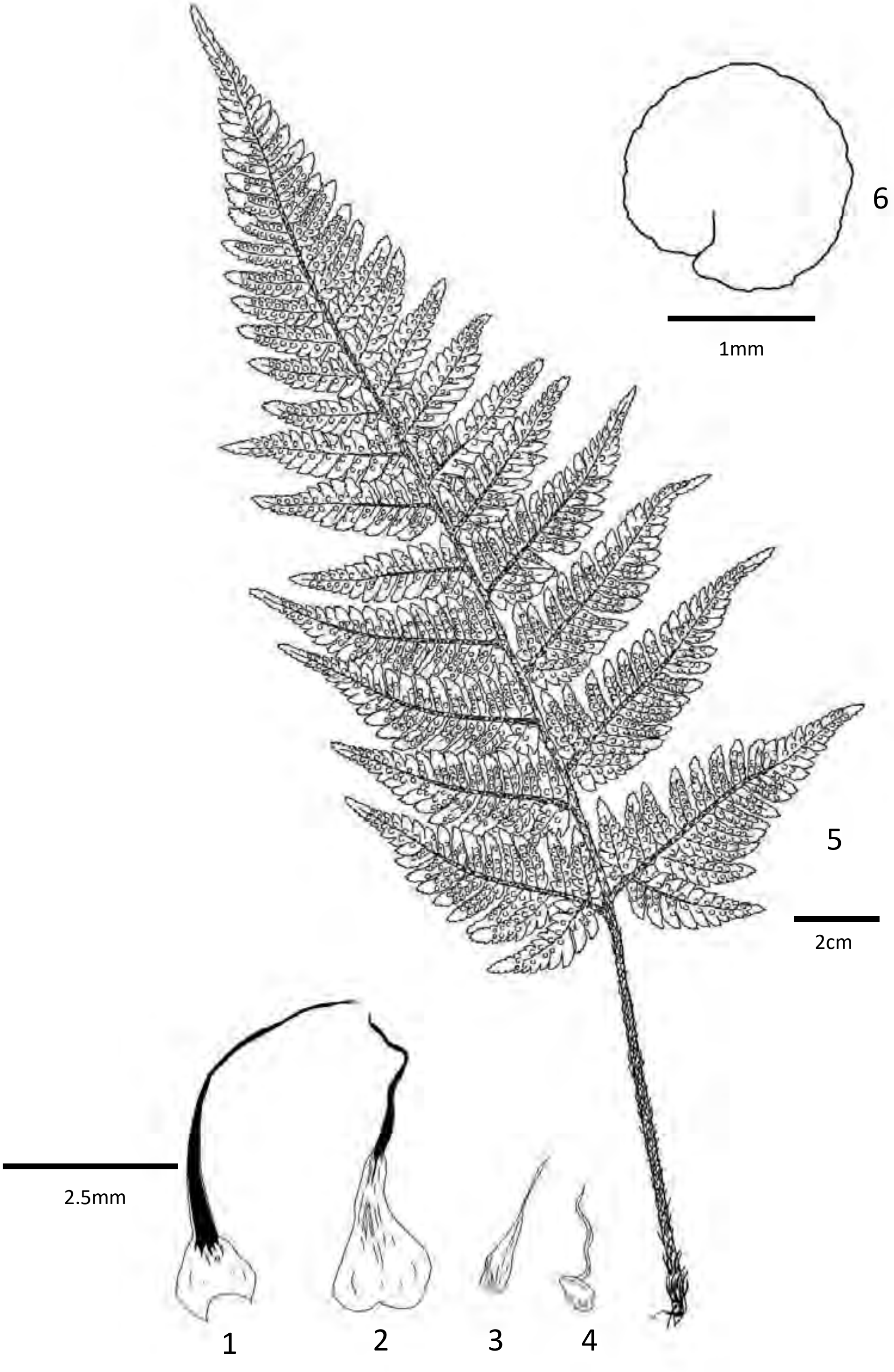


FIG. 8. *Dryopteris protobissetiana* K. Hori et N. Murak. 1–4: Scales at base of petiole, upper petiole, rachis and costa. 5: Frond; abaxial surface. 6: indusium. (drawn from type specimen, *K. Hori 906*, MAK).

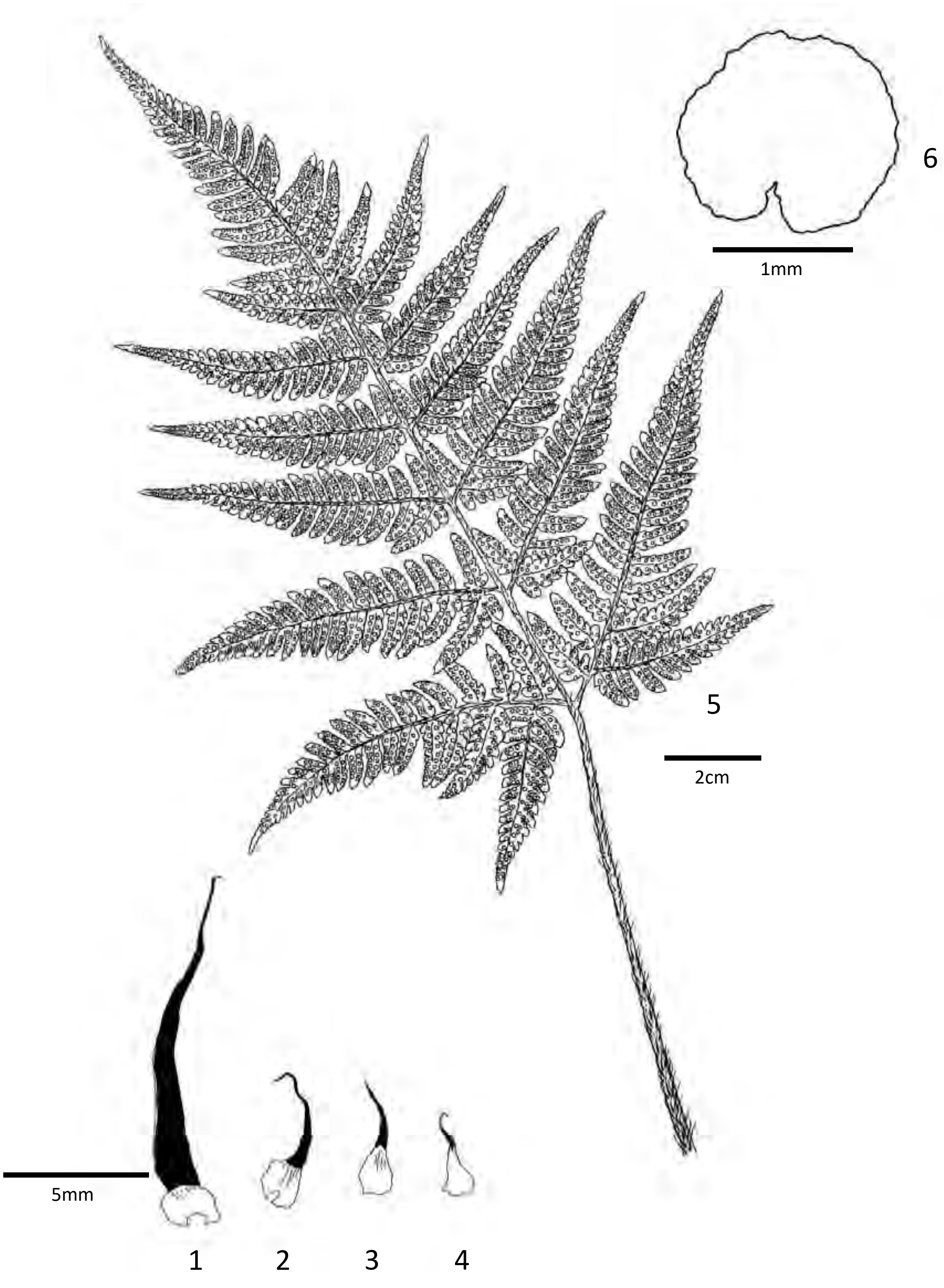


FIG. 9. *Dryopteris sacrosancta* Koidz. 1–4: Scales at base of petiole, upper petiole, rachis and costa. 5: Frond; abaxial surface. 6: indusium. (drawn from the specimen o*f K. Hori & Y. Inoue 490*, MAK).

9. Dryopteris saxifraga H. Itô in Bot. Mag. Tokyo. 50: 125 (1936). —Fig. 10

Type: Japan, Shizuoka Pref. or Yamanashi Pref., Hujisan [Fuji-san] (*B. Hayata F3*, TI). — *Dryopteris varia* subsp. *saxifraga* (H. Itô) Sugim., Keys Herb. Pl. Jap. Pterid. 282, 405. 1966. — *Dryopteris varia* var. *saxifraga* (H. Itô) H. Ohba in Sci. Rep. Tohoku Univ. B 36: 111. 1971.

Herbs, terrestrial, evergreen; rhizome erect or slightly ascending. Leaves cespitose; scales dense on rhizome, petiole, rachis and costa; petiole 5–20 cm long; scales lanceolate, deflexed, apex filiform; scales at base of petiole black, flat, spreading, base brown; scales on upper petiole, rachis and costa usually black, rarely brown, base bullate and brown; lamina bipinnate, occasionally tripinnate at base, oblong, gradually narrowing to apex, 5–30 cm long, 5–15 cm wide, whitish green, soft coriaceous, surface dull, margins recurved; pinnae curved, apex obtuse; pinnules obtuse, apical margin entire or sinuate; lowest basiscopic pinnules on lowest pinna barely longer than second basiscopic pinnule; sori round, medial; indusia reniform or circular, margins entire or erose, translucent, 1.5–2 mm in diameter; spores per sporangium 64; chromosome number $2n = 82$ (Fig. 13j), diploid sexual.

Notes. Lee & Park (2006) reported the triploid apogamous cytotype of *Dryopteris saxifraga* from South Korea. Lee & Park (2013) reported sequences of nuclear *PgiC* from the triploid apogamous *D. saxifraga*, which formed a clade with the diploid sexual *D. saxifraga* in their *PgiC* molecular tree. *Dryopteris bissetiana* is sometimes similar to *D. saxifraga* in gross morphology because *D. bissetiana* is of hybrid origin between *D. saxifraga* and *D. protobissetiana*. The samples of Lee & Park (2013) were confirmed to be triploid apogamous. Only diploid sexual cytotypes have been found in *D. saxifraga* in Japan. These facts suggest that the triploid apogamous *D. saxifraga* in Lee & Park (2013) might be *D. bissetiana*.

Habitat and distribution. Deciduous broadleaved forests. Japan (Hokkaido, Honshu, Shikoku and Kyushu) (Fig. 14-2i), Korea, and northeast China.

Japanese name. Iwa-Itachishida.

Notes. Dryopteris saxifraga, a sexual diploid with a distinct genome, is characterized by having pinnules with entire margins and oblong lamina.

Specimens examined. **JAPAN.** HOKKAIDO. **Hokkaido Pref.:** Asahikawa city, Kamui, *K. Horie s.n.*, Jun. 5, 1994 (TNS). HONSHU. **Aichi Pref**.: Kitashitara county, *K. Hori 1131* (MAK). **Akita Pref.:** Sennboku city, Dakigaeri velley, *K. Hori & Y. Horii 1494* (MAK); *K. Hori & Y. Horii 1496* (MAK). **Aomori Pref.:** Aomori city, Mie fall, *T. Sudo s.n*., Oct. 3, 1982 (TNS). **Fukui Pref.:** Mikata county, Mihama town, Oct. 9, 1979 (TNS). **Fukushima Pref.:** Aizuwakamatsu city, Higashiyama town, *Z. Kaneda 5342* (TNS). **Gifu Pref.:** Ena city, Iiji town, *T. Ogiyama 9866* (TNS). **Gunnma Pref.:** Agatsuma county, Kuni village, *A. Yamamoto s.n*., Aug. 2, 1983 (TNS). **Hiroshima Pref.:** Hiba county, Saijo town, Mt. Hiba, *T. Takeda 963* (TNS). **Hyogo Pref.:** Kita Ward, Mt. Rokkosann, *T. Shiraiwa 9839* (TNS). **Ibaraki Pref.:** Hitachi city, Mt. Takasuzu, *M. Yasu s.n*., Jun. 12, 1977 (TNS). **Ishikawa Pref.:** Hakui county, Shika town, *S. Komaki s.n.,* May. 20, 1976 (TNS). **Iwate Pref.:** Hanamaki city, Hanamakionnsenn, *Y. Nakaima s.n*., Oct. 4, 1981 (TNS). **Kanagawa Pref.:** Ashigarakami county, Yamakita town, *T. Sato s.n*., Jan. 3, 1982 (TNS). **Mie Pref.:** Iinami county, Iidaka town, *Y. Higuchi s.n*., Sep. 9, 1973 (TNS). **Miyagi Pref.:** Katta county, Zaou town, *Y. Takeichi s.n*., Aug. 13, 1982 (TNS). **Nagano Pref.:** Azumi village, Norikurakougenn, *K. Otsuka 8466* (TNS). **Nara Pref.:** Yoshino county, Tennkawa village, *F. Kasetani 669-1* (TNS). **Niigata Pref.:** Shibata city, Akaya, *F. Konta 405* (TNS). **Okayama Pref.:** Atetsu county, Oosa town, *H. Kobatake & S. Kariyama s.n*., *Oct. 15*, *1984* (TNS). **Osaka Pref.:** Minamikawachi county, Chihaya-akasaka village, *I. Yamazumi IY027* (TNS). **Saitama Pref.:** Chichibu city, Urayama, *T. Iwata 36332* (TNS). **Shiga Pref.:** Shiga county, Shiga town, *T. Shiraiwa 1442* (TNS). **Shimane Pref.:** Iiishi county, Iinann town, Tonnbara, *M. Yagiura 156-15* (TNS). **Shizuoka Pref.:** Fuji city, Imamiya, *T. Hosokura s.n*., Aug. 3, 1987 (TNS). **Tochigi Pref.:** Kamitsuga county, Ashio town, *K. Ogawa s.n*., Aug. 19, 1957 (TNS). **Tokyo Pref.:** Akiruno city, *K. Hori 1107* (MAK). **Tottori Pref.:** Tottori city, Saigou village, *H. Tanioka s.n*., Aug. 12, 1957 (TNS). **Toyama Pref.:** Uotsu city, Toradani, *T. Oshima s.n*., Aug. 3, 1977 (TNS). **Yamagata Pref.:** Akumi county, Hirata town, *S. Kato s.n*., Apr. 29, 1972 (TNS). **Yamanashi Pref.:** Ennzann city, *A. Yamamoto s.n*., Aug. 18, 1981 (TNS). SHIKOKU. **Kochi Pref.:** Nagaoka county, Ootoyo town, *Y. Yamamoto s.n*., Sep. 15, 1981 (TNS).

KYUSHU. **Fukuoka Pref.:** Buzenn city, Mt. Inugatake, *N. Inoue 3107* (TNS). **Kagoshima Pref.:** Aira county, Makizono town, *K. Takesako s.n.*, Oct. 1975 (TNS). **Kumamoto Pref.:** Aso county, Minamioguni town, *T. Kariyazaki s.n.*, Aug. 7, 1984 (TNS). **Miyazaki Pref.:** Higashiusuki county, Morozuka village, *Y. Akagi s.n.*, *MZC774* (TNS). **Nagasaki Pref.:** Minamitakaki county, Obama town, Mt. Unnzenn, *B. Matsubayashi s.n.*, Nov. 9, 1980 (TNS). **Oita Pref.:** Beppu city, Inoseto, *M. Arakane s.n.*, Nov. 6, 1955 (TNS).

CHINA. **Liaoning Prov.:** Mt. Fenghuang *J. Z. Wang 81016* (PE).

KOREA. **Cheju Special Autonomous Prov.:** Chejudo, *I. C. Chung 1611* (TNS).

10. **Dryopteris subhikonensis** K. Hori & N. Murak., **sp. nov.** —Fig.11

Dryopteris subhikonensis K. Hori & N.Murak. is an apogamous species of hybrid origin between *D. hikonensis* and *D. saxifraga* or between *D. bissetiana* and *D. varia*. Its genome consists of those from *D. protobissetiana*, *D. saxifrage*, and *D. varia.* It is hardly distinguishable from *D. hikonensis* based only on morphology. It is therefore recommended that the nuclear DNA constitution be determined before reporting new localities. *Dryopteris subhikonensis* usually differs from *D. hikonensis* in having shallowly serrate or entire pinnules, as well as entire indusia. *Dryopteris hikonensis* is common in forests along the Pacific Ocean and Seto Inland Sea, whereas *D. subhikonensis* is in the mountains in southeastern Honshu and in forests along the Sea of Japan.

Typus: Japan, Saitama, Han-nou City, Shirako, 200 m, on soil cliff near dry road in forests, *K. Hori 2270*, July 2, 2016 (holo-, MAK 449117).

Herbs, terrestrial, evergreen; rhizome erect or slightly ascending. Leaves cespitose; scales dense on rhizome, petiole, rachis, and costa; petiole 10–40 cm long; scales lanceolate, apex filiform; scales at base of petiole and upper petiole black, flat, narrow, base brown; scales on rachis black, flat, spreading, base brown; scales on costa brown, bullate; lamina bipinnate, occasionally tripinnate at base, widely triangular, sub-abruptly narrowing to apex, 20–50 cm long, 10–30 cm wide, dark green, soft coriaceous, surface weakly shiny, margin flat; pinnae curved, apex acute; apical margins of pinnules shallowly serrate or entire; lowest basiscopic pinnules on lowest pinna slightly longer than second basiscopic pinnule; sori round, medial; indusia reniform or circular, margins entire, translucent, approximately 1.5–1.8 mm in diameter; spores per sporangium 32; chromosome number $2n = 123$ (Fig. 13k), triploid apogamous.

Habitat and distribution. Warm temperate evergreen forests and secondary forests in temperate zone. Endemic in Japan (southeastern and south Japan sea side of Honshu) (Fig. 14-2j).

Japanese name. Iwa-O-Itachishida.

Specimens examined. **JAPAN.** HONSHU. **Aichi Pref.:** Kitashitara county, Touei town, *K. Hori 2469* (MAK). **Akita Pref.:** Kisakata town, Osugo, *Y. Horii s.n.*, Jul. 22, 1989 (TNS). **Chiba Pref.:** Chiba city, Sawa town, *I. Ueda s.n.*, Aug. 15, 1981 (TNS). **Fukui Pref.:** Nanjo county, Minamiechizen town, Kaburagi, *K. Hori 1484* (MAK). **Gifu Pref.:** Ena city, Kamiyahagi town, Hiraiwa, *T. Ogiyama 9368* (TNS). **Gunnma Pref.:** Kannra county, Shimonita town, Abuta, *S. Kojima s.n.*, Oct. 29, 1983 (TNS). **Hiroshima Pref.:** Hiba county, Saijo town, Hogaya, *T. Takeda 2924* (TNS). **Hyogo Pref.:** Kisaki county, Kasumi town, Hayato, *Y. Hayashi s.n.*, May. 25, 1976 (TNS). **Ishikawa Pref.:** Hakui city, Yanagida, *S. Komaki s.n.*, Sep. 21, 1975 (TNS). **Kanagawa Pref.:** Sagamihara city, Midori Ward, Obara, *K. Hori 2287* (MAK). **Kyoto Pref.:** Amata county, Sannwa town, Nakaide, *T. Nakaike s.n.*, Aug. 8, 1983 (TNS). **Miyagi Pref.:** Watari county, Watari town, Nagatoro, *K. Shogo & O. Asano s.n.*, Sep. 25, 1983 (TNS). **Nagano Pref.:** Shimoina county, Anann town, *K. Hori 2463* (MAK). **Niigata Pref.:** Sado city, Aikawa, *M. Saito s.n.*, Nov. 11, 1987 (TNS). **Okayama Pref.:** Takahashi city, Bittyuu town, *T. Oka & K. Hori 2599* (MAK). **Saitama Pref.:** Hannno city, *K. Hori 2270* (MAK). **Shiga Pref.:** Takashima city, Katsuno, *K. Hori 2427* (MAK). **Shimane Pref.:** Goutsu city, Matsukawa town, Oota, *Y. Shinohara 8399* (TNS). **Shizuoka Pref.:** Hamamatsu city, Tenryuu Ward, Sakuma town, Urakawa, *K. Hori 2416* (MAK). **Tochigi pref.:** Tochigi city, Mt. Boroishi, *K. Ogawa s.n.*, Jun. 2, 1962 (TNS). **Tokyo Pref.:** Akiruno city, Youzawa, *K. Hori 1146* (MAK). **Tottori Pref.:** Hino county, Ebu town, Matano, *M. Aoto s.n.*, Sep. 7, 1980 (TNS). **Toyama Pref.:** Oyabe city, Komoridani, *T. Oshima s.n.*, Aug. 5, *1984* (TNS). **Yamaguchi Pref.:** Hagi city, Susa, *H. Akimaru 20130193* (TNS).

11. **Dryopteris varia** (L.) Kuntze, Revis. Gen. Pl. 2: 814. 1891. —Fig. 12

Polypodium varium L., Sp. Pl. 2: 1090. 1753. Type: China, *P. Osbeck. s.n.*, 1.1.9.75, SBT! — neo- designated

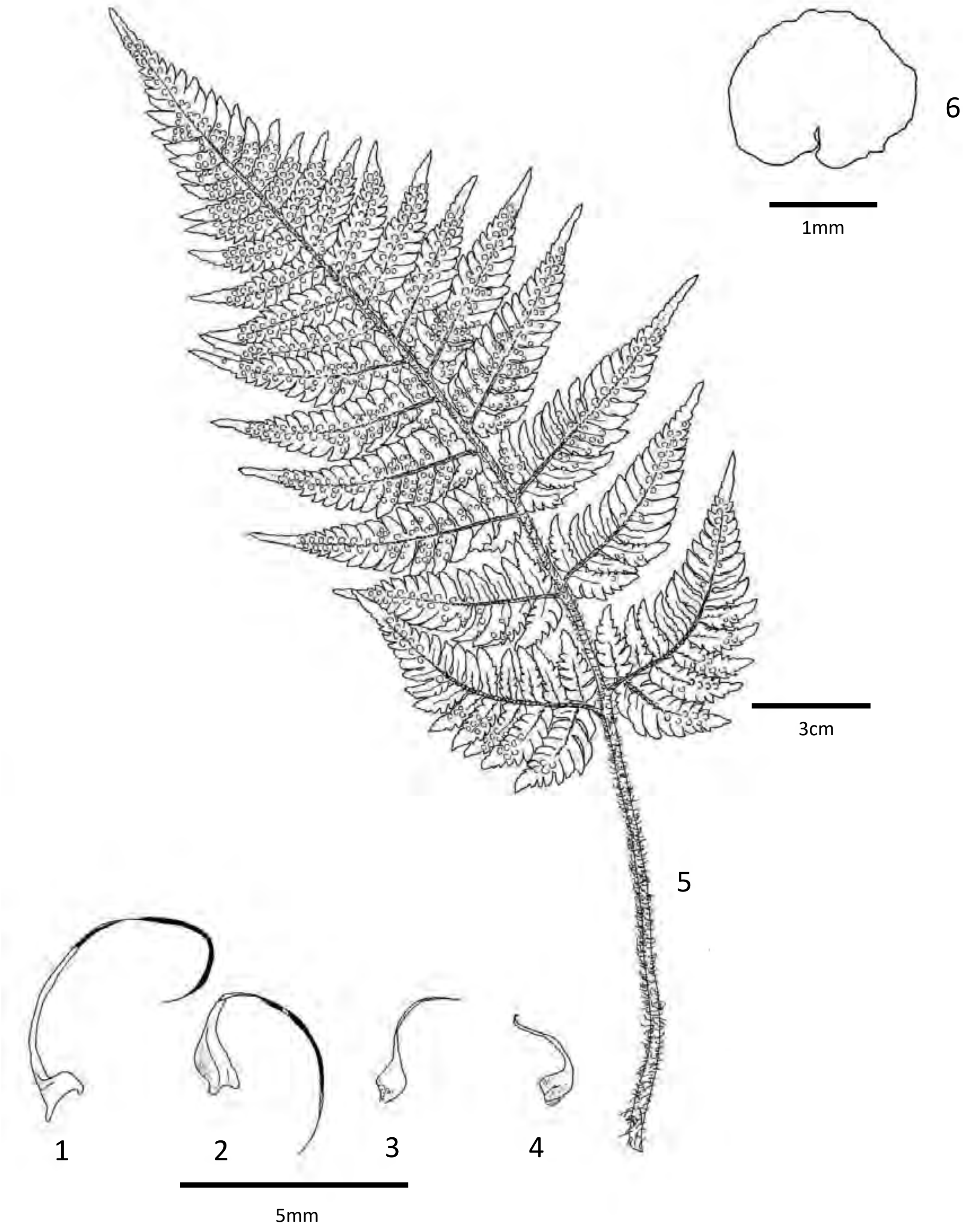


Fig. 10. *Dryopteris saxifraga* H. Itô 1–4: Scales at base of petiole, upper petiole, rachis and costa. 5: Frond; abaxial surface. 6: indusium. (drawn from *K. Hori & Y. Horii 1494*, MAK).

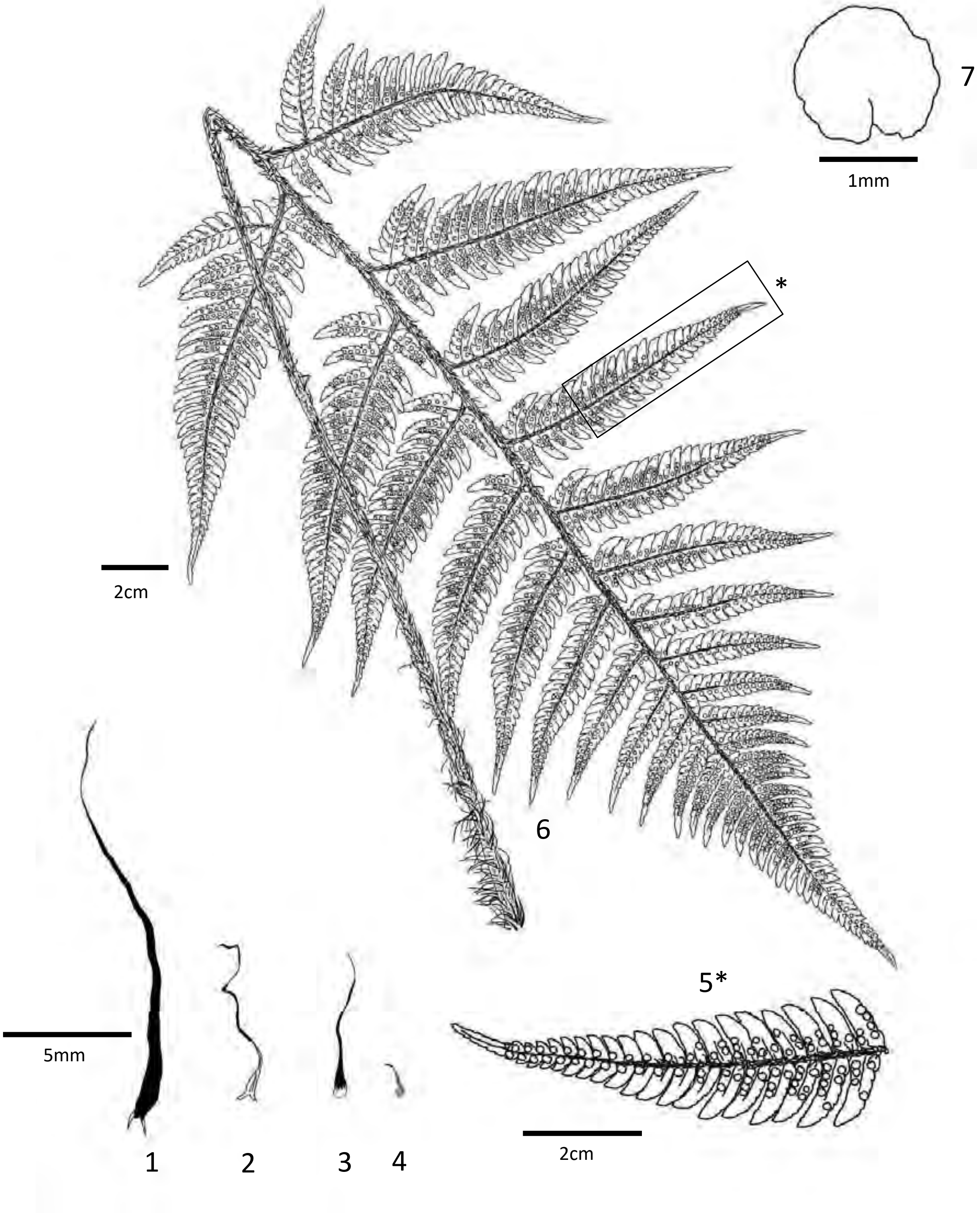


FIG. 11. *Dryopteris subhikonensis* K. Hori et N. Murak. 1–4: Scales at base of petiole, upper petiole, rachis and costa. 5: Frond; abaxial surface of upper pinnae. 6: abaxial surface. 7: indusium. (drawn from type specimen, *K. Hori 2270*, MAK).

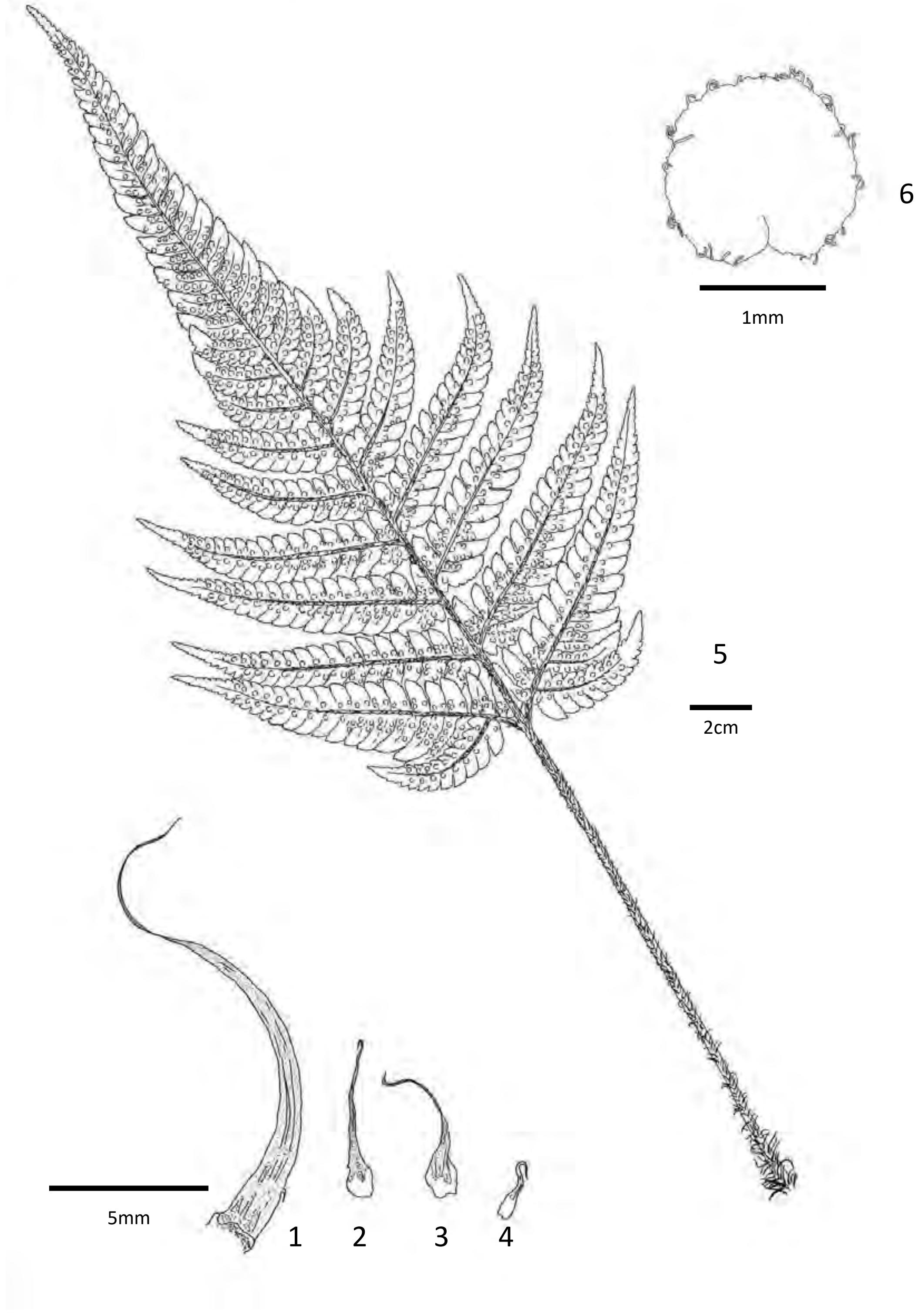


FIG. 12. *Dryopteris varia* (L.) Kuntze 1–4: Scales at base of petiole, upper petiole, rachis and costa. 5: Frond; abaxial surface. 6: indusium. (drawn from *K. Hori 1387*, MAK).

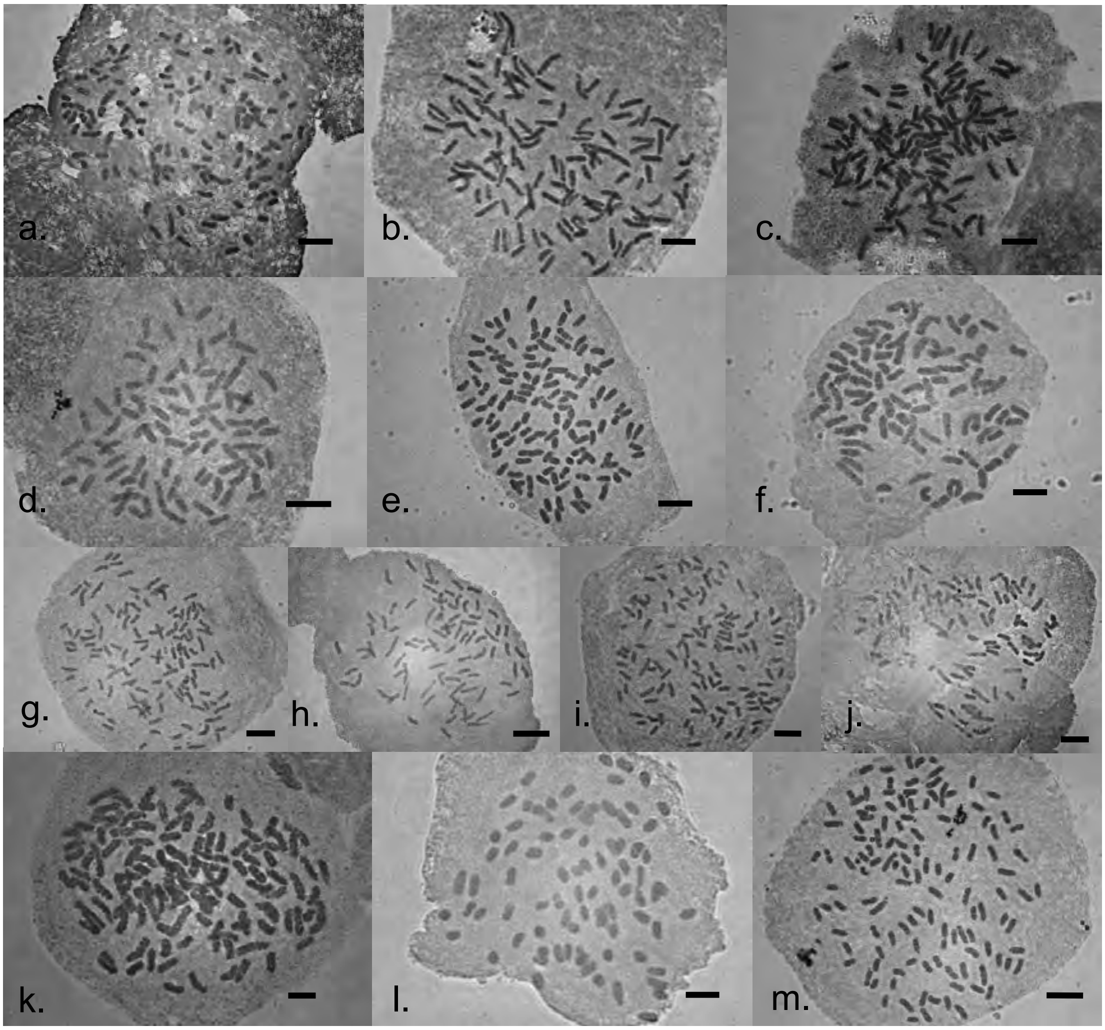


FIG. 13. Mitotic metaphase chromosomes of the *Dryopteris varia* complex. a, *D. bissetiana*, 2*n* = 123, *K. Hori 532*; b, *D. chichisimensis*, 2*n* = 123, *K. Hori 1351*; c, *D. erythrovaria*, 2*n* = 123, *K. Hori 485*; d, *D. hikonensis*, 2*n* = 82, *K. Hori 531*; e, *D. hikonensis*, 2*n* = 123, *K. Hori 517*; f, *D. insularis*, 2*n* = 82, *K. Hori 1350*; g, *D. kobayashii*, 2*n* = 123, *K. Hori 8*; h, *D. protobissetiana*, 2*n* = 82, *K. Hori 1756*; i, *D. sacrosancta*, 2*n* = 123, *K. Hori 490*; j, *D. saxifraga*, 2*n* = 82, *K. Hori 1496*; k, *D. subhikonensis*, 2*n* = 123, *K. Hori 1146*; l, *D. varia*, 2*n* = 82, *K. Hori 1393*; m, *D. varia*, 2*n* = 123, *K. Hori 495*. Scale bar: 5 µm. All voucher specimens deposited in MAK.

by Mazumdar in Nord. J. Bot. 34. 466-467. 2016. — *Aspidium varium* (L.) Sweet in Schrad. J. Bot. 1800–2: 35. 1801. — *Nephrodium varium* (L.) C. Presl Reliq. Haenk. 1. 36. 1825. — *Polystichum varium* (L.) C. Presl in Abh. Königl. Böhm. Ges. Wiss., ser. 5. 1851. c *Lastrea varia* (L.) T. Moore, Ind. Fil. 107. 1858.

Lastrea opaca Hook. in Hooker's J. Bot. 9: 339 (1857). Type: Hong Kong and mainland N. W. of Hong Kong, *J. C. Bowman s.n.* K! – lecto-, designated by C. R. Fraser-Jenkins in Bull. Brit. Mus. Nat. Hist (Bot). 18: 432. 1989. — *Aspidium opacum* (Hook.) Benth., Fl. Hongk.: 456 (1861).

Nephrodium coriaceum C. Hope in J. Bot., London 28: 328, 1890. Type: India, Kapili Hot Springs, North Cachar Hills, Assam, 1000 ft, February 1890, *G. Mann s.n.*, K – lecto-; BM, DD, E, K, P, PE — isolecto-, designated by Fraser-Jenkins in Bull. Brit. Mus. Nat. Hist (Bot). 18: 432. 1989.

Dryopteris yabei Hayata in J. Coll. Sci. Imp. Univ. Tokyo 30: 424. 1911. Type: Taiwan, Kushaku and Shintengai (*K. Miyake s.n.*, 1899, TI — holo-). — *Dryopteris*

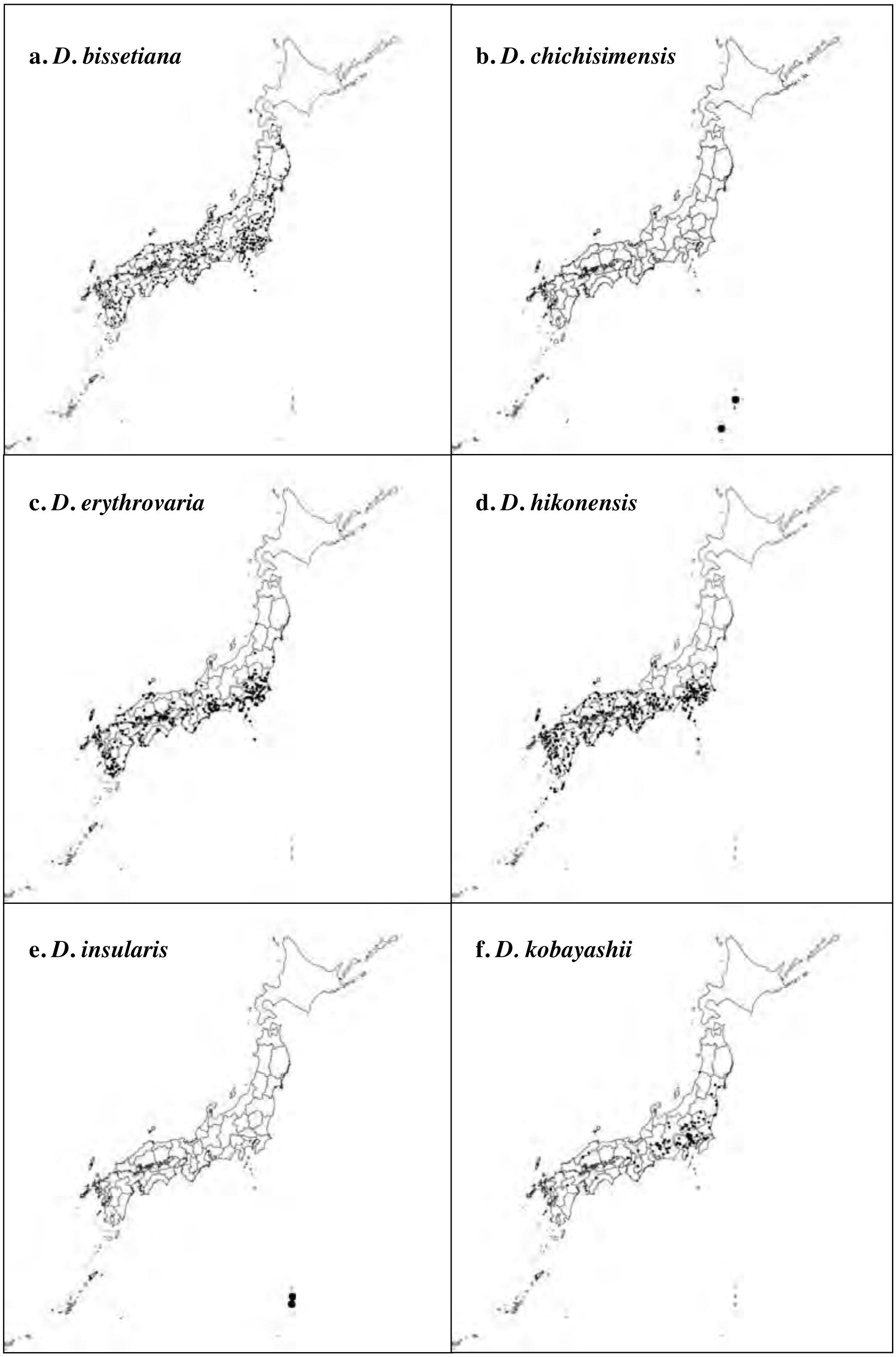
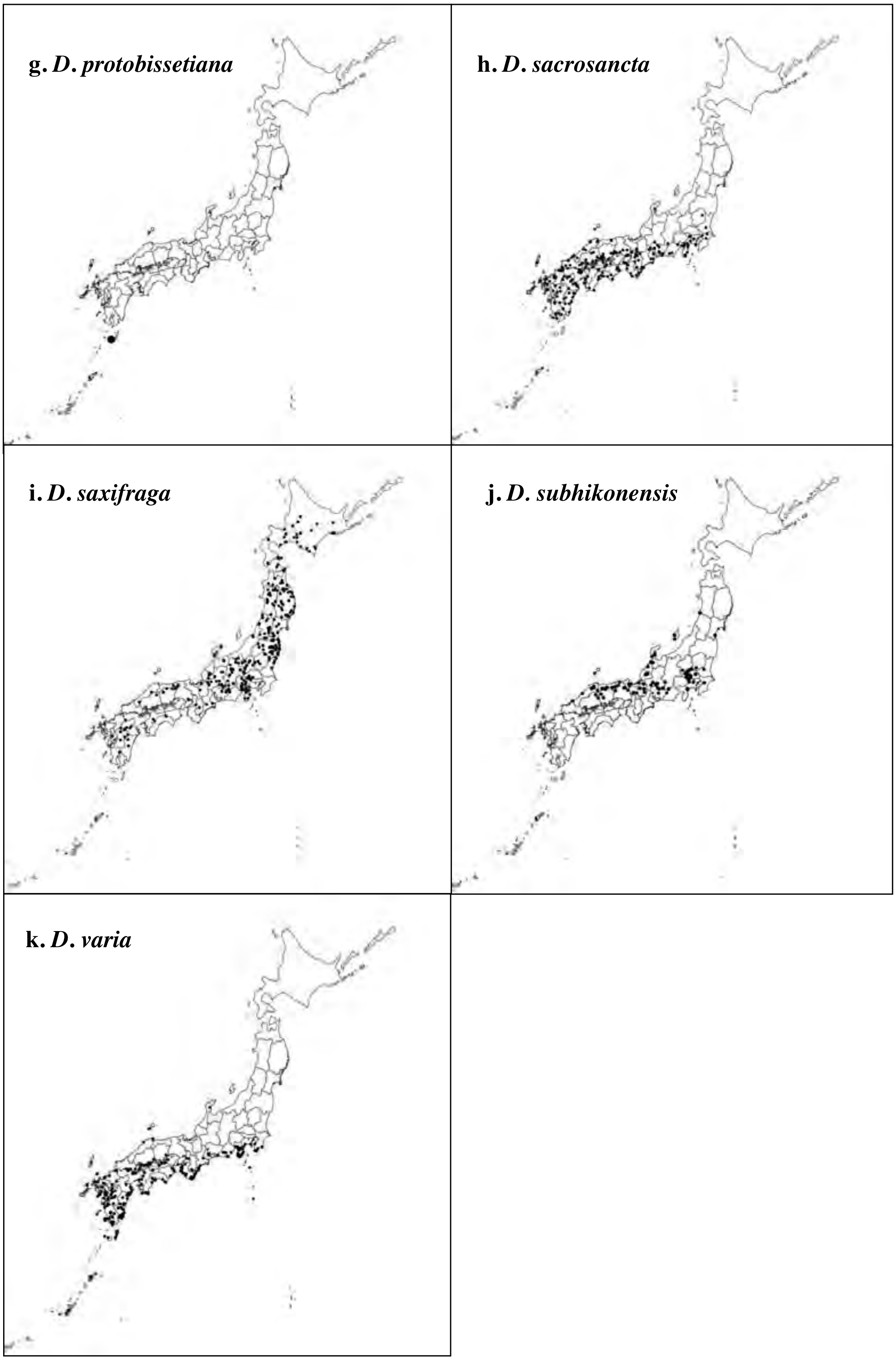


FIG. 14-1. Distribution maps of the *Dryopteris varia* complex in Japan. a, *D. bissetiana*; b, *D. chichisimensis*; c, *D. erythrovaria*; d, *D. hikonensis*; e, *D. insularis*; f, *D. kobayashii.*



g. *D. protobissetiana*

h. *D. sacrosancta*

i. *D. saxifraga*

j. *D. subhikonensis*

k. *D. varia*

FIG. 14-2. Distribution maps of the *Dryopteris varia* complex in Japan. g, *D. protobissetiana*; h, *D. sacrosancta*; i, *D. saxifraga*; j, *D. subhikonensis*; k, *D. varia*.

yabei f. *typica* H. Itô in Nakai et Honda, Nova Fl. Jap. 4: 59. 1939.

Polystichum hololepis Hayata, Icon. Pl. Formosan. 5: 332. 1915. Type: Taiwan, Taihoku (*T. Ito & S. Fujii s.n.*, TI — holo-). —*Dryopteris yabei* var. *hololepis* (Hayata) H. Itô in Bot. Mag. Tokyo 50: 128. 1936.

Dryopteris matsuzoana Koidz. in Bot. Mag. Tokyo 39: 15. 1925. Type: Japan, Prov. Iyo (Ehime Prefecture), Minamiuwa-gun, Shimonadamura and Jinadamura (*M. Ogata s.n.*, KYO — holo-). — *Dryopteris yabei* var. *matsuzoana* (Koidz.) H. Itô in Bot. Mag. Tokyo 50: 128. 1936.

Dryopteris ogawae H. Itô in Nakai, Iconogr. Pl. Asiae Orient. 1: 18. Pl. 9. 1935. (as ‘oagwai’) Type: Prov. Awa (Chiba Prefecture), Kiyozumiyama (*M. Kishida s.n.*, Apr. 1933, TI — holotype). — *Dryopteris yabei* var. *ogawae* (H. Itô) H. Itô in Bot. Mag. Tokyo 50: 128. 1936. — *Dryopteris yabei* f. *ogawae* (H. Itô) H. Itô in Nakai et Honda, Nova Fl. Jap. 4: 59. 1939.

Dryopteris nanchuanensis Ching & Z. Y. Liu in Bull. Bot. Res., Harbin 4 (4): 9, f. 37. 1984. Type: China, Sichuan, Nanchuan, Jinfoshan (*Z. Y. Liu 3828* — holo-).

Dryopteris sinobissetiana Ching & Z. Y. Liu in Bull. Bot. Res., Harbin 4 (4): 8, f. 36. 1984. **syn. nov.** Type: China, Sichuan, Nanchuan, Jinfoshan (*Z. Y. Liu 4291*, *Feb. 23*, *1983*, PE 1119057 — holo-).

Dryopteris caudifolia Ching & P. C. Chiu in Bot. Res. Academia Sinica 2: 21, t. 8, f. 2. 1987. Type: China, Guangxi, Lung-sheng Xian (*P. C. Chiu 4682*, PE — holo-).

Dryopteris lingii Ching in Bot. Res. Academia Sinica 2: 23, t. 8, f. 4. 1987. Type: China. Fujian, Ning-yang Xian (*Y. Ling s.n.*, Dec. 1932, PE — holo-).

Dryopteris glabrescens Ching & P. C. Chiu ex K. H. Shing & J. F. Cheng in Jiangxi Sci. 8(3): 48. 1990. Type: China, Jiangxi, Li Shan, Xiufeng (*P. C. Chiu 3157*, Jul 25, 1963, PE — holo-).

Dryopteris pseudobissetiana Ching ex K. H. Shing & J. F. Cheng in Jiangxi Sci. 8(3): 49. 1990. **syn. nov.** Type: China, Jiangxi, Lushan (*R. C. Ching 11357*, June 7, 1935, PE1863702 — holo-).

Herbs, terrestrial, evergreen; rhizome erect or slightly ascending. Leaves cespitose; scales dense on rhizome, petiole, rachis, and costa; petiole 10–40 cm long; scales brown, lanceolate, ascending, apex filiform; base of scales at base of petiole flat, narrow; base of scales on upper petiole, rachis, and costa flat, spreading; lamina bipinnate, occasionally tripinnate at base, pentagonal to widely triangular, abruptly narrowing to apex, 20–40 cm long, 10–30 cm wide, dark, yellowish or whitish green, hard coriaceous, surface shiny to dull, margin flat; pinnae curved, apex acute; pinnules acute, entire, apical margin shallowly finely or deeply serrate; lowest basiscopic pinnules on lowest pinna much longer than second basiscopic pinnule; sori round, medial; indusia reniform or circular, margins entire or ciliate, translucent, 1.5–1.8 mm in diameter; spores per sporangium 32 or 64; chromosome number $2n = 82$ (Ebihara *et al.* 2014, diploid sexual, known only from Taiwan, Fig. 13l) or 123 (triploid apogamous, Fig. 13m).

Habitat and distribution. Warm temperature to subtropical evergreen forests and secondary forests in temperate to subtropical zones. Japan (Honshu, Shikoku, Kyushu and Ryukyu) (Fig. 14-2k.), Korea, China, Taiwan, India, Thailand, Indochina and the Philippines.

Japanese name. Nankai-Itachishida.

Notes. Dryopteris varia is variable in morphology, but can be characterized by having the apex of the lamina abruptly narrowed, the hard coriaceous texture of the lamina and flat scales. Infraspecific cytological variation was observed in this species, but the genome constitution differs from other members of the *D. varia* complex.

Tsai & Shieh (1975, 1985) reported a tetraploid sexual cytotype of *Dryopteris varia* from Taiwan. However, even though Ebihara *et al.* (2014) and we (present study) reexamined the cytology of several individuals of *D. varia* from the same localities in Taiwan, we never found tetraploid cytotypes.

Dryopteris caudifolia, *D. glabrescens*, *D. lingii* and *D. nanchuanensis* were treated as synonyms of *D. varia* by Zhang *et al.* (2013), while *D. sinobissetiana* and *D. pseudobissetiana* were treated as synonyms of *D. setosa* in Zhang *et al.* (2013). These names can be regarded as synonyms of *D. varia* based on morphological characteristics. The genome constitution of *D. varia* in China need further investigation.

Specimens examined. **JAPAN.** HONSHU. **Aichi Pref.:** Chita county, Mihama town, Noma, *K. Inukai s.n.*, Jan. 3, 1971 (TNS). **Chiba Pref.:** Awa county, Chikura town, Mt. Takatsukayama, *N. Sahashi s.n.*, May. 4, 1971

(TNS). **Hiroshima Pref.:** Innoshima Is., *K. Hori 330* (MAK). **Hyogo Pref.:** Sumoto city, Nakatsugawagumi, *K. Mune s.n.*, Jul. 29, 1947 (TNS). **Kanagawa Pref.:** Ashigarashimo county, Manazuru town, *T. Date 13202* (TNS). **Mie Pref.:** Minamimuro county, Kihou town, Ida, *K. Hori 154* (MAK). **Nara Pref.:** Yoshino county, Totsukawa village, Tano, *Z. Tsujimoto s.n., s.n.*, Sep. 26, 1994 (TNS). **Okayama Pref.:** Bizen city, Ootaki, Fukuoji temple, *T. s.n.*, Jan. 27, 1978 (TNS). **Osaka Pref.:** Habikino city, Furuichi town, *T. Kodama s.n.*, Aug. 1950 (TNS). **Shiga Pref.:** Hino town, Mt. Yotsugase, *C. Hashimoto s.n.*, Nov. 10, 1956 (TNS). **Shimane pef.:** Oki Islands, *H. Ito s.n.*, Jul. 30, 1963 (TNS). **Shizuoka Pref.:** Kamo county, *K. Hori 107* (MAK). **Tokyo Pref.:** Aogashima Island., *Y. Jotani s.n.*, Jul. 20, 1958 (TNS). **Wakayama Pref.:** Higashimuro county, Taiji town, *K. Hori 118* (MAK). **Yamaguchi Pref.:** Boufu city, Mukoujima Island, *S. Miyake s.n.*, *Oct. 19*, *17725* (TNS). SHIKOKU. **Ehime Pref.:** Araihama city, *H. Ishikawa 234* (TNS). **Kagawa Pref.:** Takamatsu city, Kinashi town, *K. Hori 511* (MAK). **Kochi Pref.:** Tosashimizu city, *K. Tanaka & K. Hori 188* (MAK). **Tokushima Pref.:** Anann city, Mt. Tiryuuji, *T. Nakayama 634* (TNS). KYUSHU. **Fukuoka Pref.:** Itoshima county, Shima town, *S. Tsutsui 13467* (TNS). **Kagoshima Pref.:** Aira city, Fukuyama town, Isowaki, *K. Takesako 3947* (TNS). **Kumamoto Pref.:** Uki city, *K. Hori 652* (MAK). **Miyazaki Pref.:** Higashimorokata county, Takaoka town, Kusumi, *T. Minamitani 20090* (TNS). **Nagasaki Pref.:** Nagasaki city, Mogi, *S. Tsutsui 9738* (TNS). **Oita Pref.:** Hita city, Akibaru town, *S. Tsutsui 13995* (TNS). **Saga Pref.:** Kashima city, *Y. Inoue & K. Hori 495* (MAK). RYUKYU. **Okinawa Pref.:** Kumejima Island, *T. Amano 7076* (TNS).

CHINA. **Chonqing city.:** Nanchuan, *S. Lai 354* (PE). Hainan Prov.: Mt. Zhafu, *F. S. Wuzhishan 552* (PE).

KOREA. **Cheju Special Autonomous Prov.:** Cheju-do, *S. Matsumoto KR-053* (TNS).

TAIWAN. **Taipei city.:** Urai, *K. Hori 1387* (MAK); *K. Hori 1393* (MAK).

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